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HEREDITAS

GENETISKT ARKIV

UTGIVET AV MENDELSKA SÄLLSKAPET I LUND

REDAKTÖR: ROBERT LARSSON

BAND XXXII HÄFT. 2

LUND 1946, BERLINGSKA BOKTRYCKERIET

HEREDITAS,

a periodical devoted to the publication of original research in heredity, is published by the MENDELIAN SOCIETY at Lund, Sweden. All contributions are written in English, German or French, illustrated, when necessary, with adequate text figures and plates. Each volume contains about 500 pages, issued in four numbers.

Subscriptions should be sent to the Editor. Price *Twenty-five (25) Swedish Kronor per volume.* Post free. (The price of Vols. I—X is 10 Swedish Kronor per volume, of Vols. XI—XXIII, 15 Sw. Kr., and of Vols. XXIV—XXV 20 Sw. Kr.)

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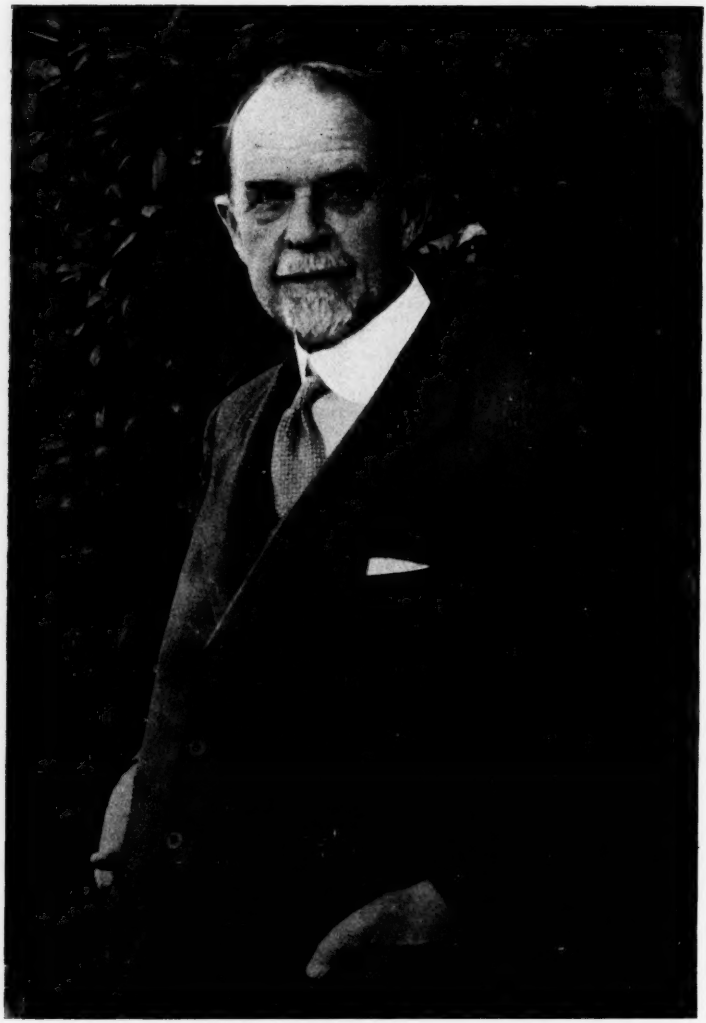

Photo taken in Stockholm, 1934

T. H. Morgan

T. H. MORGAN, Honorary Member of the Mendelian Society
In memoriam

THE GENESIS OF SOME SCANDINAVIAN SPECIES OF CALAMAGROSTIS

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I. INTRODUCTION.

THE grass genus *Calamagrostis* comprises between 150 and 250 species in all parts of the world. The delimitation of the various species is often vague, however, and what one flora author designates a species is often given only the rank of variety by another. In Europe there are at least twelve species, in Scandinavia eight.

When in 1938 it was decided to make the genus the subject of the present investigation attention was first of all confined to the European species, in the first place to the Swedish. It was soon realized that methodical cultivation experiments were necessary. Studies of plants in herbaria and in nature cannot by themselves give fully reliable results, it being desirable to compare the different species and their form-series side by side. The first material was procured from amateur botanists in various parts of Sweden. This was supplemented in later years by special journeys for purposes of personal study.

All material obtained was reared in pots for some months, after which it was planted out in the field. The plants were set about half a metre apart in rows spaced at one metre intervals. Two experimental fields have been used; as these lie only a few hundred metres from each other, the difference in weather conditions is extremely slight. The soil in both consists of clay, although this appears to be somewhat stiffer in one field than in the other. In spite of the fact that the Swedish *Calamagrostis* species grow in widely separated localities all of them except the arctic-subarctic *C. lapponica* have thriven well in cultivation.

The leading principle followed in collecting the material has been that *Nature is herself the greatest experimenter.* All material — except a single plant — is therefore derived from natural populations. Localities for the types of every species that could be of interest were found by studying the public herbaria. Personal visits were then paid to certain of these localities. In the majority of cases it was possible either to obtain a specimen of the type or to determine that it was a question of a

habitat form (especially in the case of shade types). Every effort was thus made to obtain a really representative material by collecting as many types as possible from different parts of the ranges of the various species. The non-hybrid Scandinavian material, so-called stock plants, at present consists of the following Swedish collections:

Species (Nomenclature: see HYLANDER, 1941, and pp. 186—219)	Number of types	Provinces
Calamagrostis arundinacea	26	Sc, Sm, Ög, Boh, Dal, Vrml, Uppl, Hälsl, Mpd, Jmtl.
» *canescens*	42	Sc, Sm, Srm, Boh, Dal, Uppl, Mpd, Jmtl, Nb, K Lappm.
» *epigeios*	99	Sc, Bl, Sm, Vg, Ög, Boh, Dalsl, Vrml, Dal, Hälsl, Mpd, Jmtl, Ly Lappm, T Lappm.
» *lapponica*	57	Nb, Ås Lappm, Ly Lappm, L Lappm, T Lappm, K Lappm.
» *neglecta*	61	Dalsl, Vrml, Uppl, Dal, Hälsl, Mpd, Jmtl, Vb, Nb, Ås Lappm, L Lappm, T Lappm, K Lappm.
» *chalybaea*	11	Jmtl, Ås Lappm.
» *purpurea*	174	Sm, Ög, Uppl, Dal, Hälsl, Mpd, Jmtl, Vb, Nb, Ås Lappm, Ly Lappm, L Lappm, T Lappm, K Lappm.
» *varia*	3	Gtl.

Abbreviations for names of provinces, etc.: Bl = Blekinge, Boh = Bohuslän, Dal = Dalarna, Dalsl = Dalsland, Gtl = Gotland, Hälsl = Hälsingland, Jmtl = Jämtland, K Lappm = Karesuando Lappmark, L Lappm = Lule Lappmark, Ly Lappm = Lycksele Lappmark, Mpd = Medelpad, Nb = Norrbotten, Sc = Scania, Sm = Småland, Srm = Södermanland, T Lappm = Torne Lappmark, Uppl. = Uppland, Vb = Västerbotten, Vg = Västergötland, Vrml = Värmland, Ås Lappm = Åsele Lappmark, Ög = Östergötland.

In addition to these there are some fifty natural hybrids. The chromosome numbers of the plants were successively determined, and it was soon possible to divide the species into the groups tabulated below.

Chromosome numbers of Scandinavian Calamagrostis.

Only $2n = 28$	Only $2n = 42$	Varying numbers
C. arundinacea	*C. chalybaea*	*C. epigeios* 28, 42, 56
C. canescens		*C. lapponica* 42—112
C. neglecta		*C. purpurea* 56—91
C. varia		

Counts have been previously published for three of these species. AVDULOV (1931) gives the number 28 for *C. arundinacea*, about 70 for *C. neglecta* and about

70 for *C. epigeios*; FLOVIK (1938) 28 for *C. neglecta*, ROZANOVA (1940) 28 and 56 respectively for the same species, and finally WESTERGAARD (1941) 28 and 56 respectively for C. *epigeios*. The high numbers given for *C. neglecta* are in my opinion attributable to faulty determination of the material.

Panicles were isolated from different species during the first summers the experiments were in progress. In certain cases seeds were then obtained and their germinability tested. The seeds were usually sown out in March in soil containing a little sand in wooden boxes, which had first stood in the greenhouse, then in frames in the open. The period of germination ranged from one to twelve weeks.

Progeny from isolated plants.

Species	Progeny
C. arundinacea	0
canescens	0
epigeios $2n = 28$	0
$2n = 42$	0
$2n = 56$	0 — some plants < 5 per No.
lapponica	Abundant
neglecta	Some plants < 5 per No.
chalybaea	Abundant
purpurea	Abundant
varia	0

The most striking feature of these germination tests was the great contrast between certain species. Four were self-sterile, two almost self-sterile (*C. neglecta* as well as the octoploid form of *C. epigeios*), while three gave very rich progenies irrespective of from which plants the seed was taken. (For details see Chap. IV.) These tests were combined with pollen tests (acetocarmine), the following mean values being obtained (1943):

Mean values of pollen from different Calamagrostis species.

Species	Pollen present	Morphologically good pollen
C. arundinacea	+	93,2 %
canescens	+	94,9 %
epigeios $2n = 28$	+	89,9 %
$2n = 42$	+	75,9 %
$2n = 56$	+	87,6 %
lapponica	— +	0—78 %
neglecta	+	97,8 %
chalybaea	—	0
purpurea	— (one plant has pollen)	0 (one plant = 90,7 %)
varia	+	86,0 %

The pollen of *C. epigeios* has been examined earlier by WESTERGAARD (1943). This will be discussed in Chap. IV in connexion with the fertility.

When the above results of the pollen tests were compared with the results of the previously mentioned isolation tests, it was found that just those plants which had given progeny after isolation were practically without exception devoid of pollen. From this the important conclusion could be drawn that in this case *sexual reproduction was out of the question*, as no pollen was found. Thus, these plants must be produced by *apomictic methods*. A close study of the character of the progeny and the original »sister-plants» among the stock plants also lent support to this view. (When several plants of the same species were obtained from the same locality, these were planted out successively under the designations *a*, *b*, *c*, and so on. Such plants are referred to above by the term »sister-plants».)

A comparison with the plants that had good pollen but did not give progeny after isolation furnished further support for the view advanced. In these species »sister-plants» as well as progeny exhibited variation, while those considered to be apomicts had homotypical sister-plants and a uniform progeny. This made it possible to divide the material examined into one group of *amphimictic species* and one group of *apomictic species* (TURESSON, 1926, p. 190).

Reproduction conditions in Scandinavian Calamagrostis.

Amphimictic species	Apomictic species
C. arundinacea	*C. lapponica*
canescens	*chalybaea*
epigeios	*purpurea*
neglecta	
varia	

After the reproductive conditions of the various Scandinavian *Calamagrostis* species had been clarified in their main features, a detailed investigation was carried out according to the following plan:

(1) Cytological examinations of the course of the reduction division.

(2) Embryological investigations.

(3) Taxonomical investigations on the basis of results obtained from the experimental studies.

(4) Attempts to produce artificial hybrids.

(5) Chromosome doubling attempts by the colchicine method.

(6) Attempts to produce haploids by the twin method.

(7) Ecologico-phytogeographical investigations.

The aim of the present work is to give a general survey of the Scandinavian species in the respects enumerated, leaving a discussion of the details to coming works. The ecologico-phytogeographical section, however, will be published separately and is only cursorily treated here.

II. CYTOLOGICAL STUDIES OF SCANDINAVIAN SPECIES OF CALAMAGROSTIS.

The results have reference to the material examined and must not be generalized.

1. METHOD.

All materal for studies of both mitosis and meiosis was fixed in MÜNTZING's modification of Navashin's fluid (MÜNTZING, 1932). A few root-tips were fixed in Lewitsky's fluid (8 parts of 1 % chromic acid + 2 parts of 10 % formalin). All root-tip fixations were done in Svalöf after the material had been cultivated for a time in pots. During the night before fixation the pots were cooled to + 1° C. in the refrigerating room. Fixations of reduction divisions were carried out as far as possible in nature. They were pre-treated in Carnoy with chloroform for one minute. The mateial was embedded in paraffin wax, cut into 15—30 μ slices and made permanent in Canada balsam. In a few cases P.M.C's were studied in acetocarmine. There was some difficulty in slicing the material in certain instances, especially in the case of older florets of *C. purpurea*, this being due to the high content of silicic acid in these florets. The staining was practically without exception done with gentian violet. In a few cases, however, recourse was had to crystal-violet and fuchsine-methyl green.

The drawings were performed with the aid of a drawing prism. Some of them are rather diagrammatical.

2. MITOSIS.

The form of the chromosomes is that normal for grass species. No mitotic irregularities have been observed, apart from fragments in high-chromosomal *C. lapponica*. For earlier examinations reference may be made to the introduction.

The chromosome morphology has been studied by FLOVIK on material from *C. neglecta* (1938). Such studies have been carried out by the present writer only on a minor scale.

3. MEIOSIS.

Earlier analyses have been made by FLOVIK (1938) on *C. neglecta* and by WESTERGAARD (1943) on *C. epigeios* ($2n = 28$ and 56).

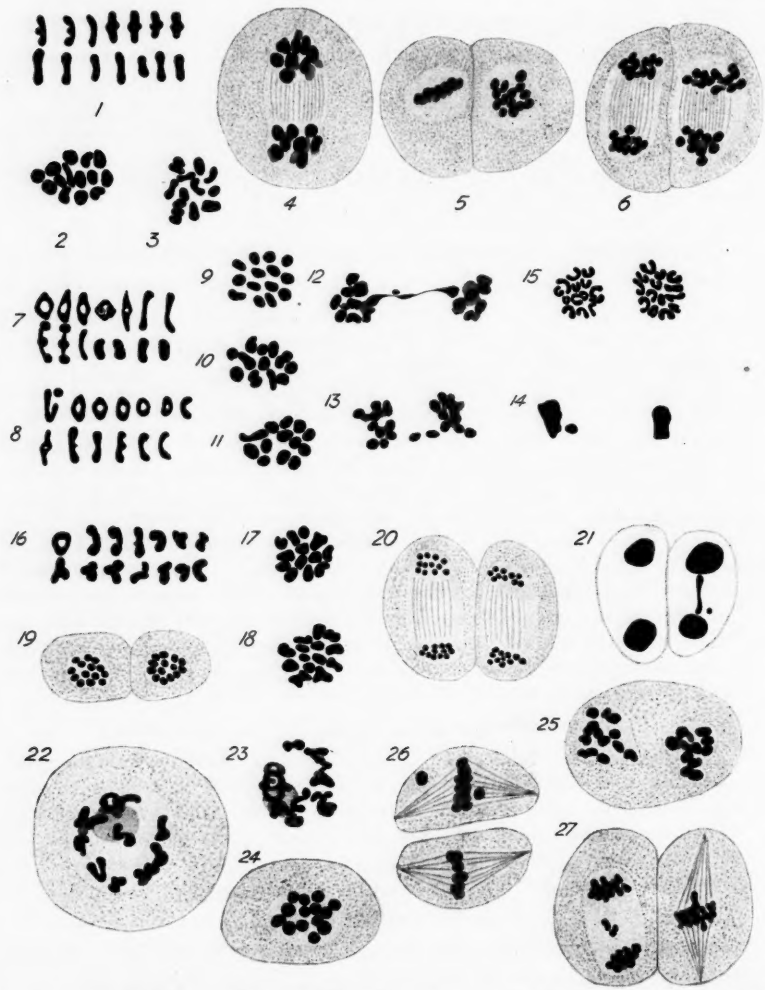
A. AMPHIMICTIC SPECIES.

a. The male side.

Calamagrostis varia.

$2n = 28$, Figs. 1—6. Material: 3 plants from Visby in Gotland.

The reduction division is regular with 14 bivalents. Only in one case has a trivalent with a univalent belonging to it been observed. The



Figs. 1—27. P.M.C's, meiosis in different species. — 1—6, *C. varia*. 1—3, first metaphase with 14 bivalents. 4, first anaphase, 5, second metaphase. 6, second anaphase. — 7—15, *C. arundinacea*. 7, 9, 10, first metaphase with 14 bivalents. 8, first metaphase with 14 bivalents. 4, first anaphase. 5, second metaphase. 6, second anabivalents at first metaphase. 12, first anaphase with inversion bridge. 13, first anaphase with late chromosomes. 14, first telophase with eliminated chromosome. 15, second metaphase. — 16—21, *C. canescens*. 16 and 18, first metaphase with 14 bivalents. 17, first metaphase with 1 quadrivalent and 12 bivalents. 19, second metaphase. 20, second anaphase. 21, second telophase with inversion bridge. — 22—27, *C. neglecta*. 22, diakinesis with 14 bivalents. 23, diakinesis with 1 quadrivalent and 12 bivalents. 24, first metaphase with 14 bivalents. 25, first anaphase. 26, second metaphase. 27, second metaphase and anaphase. — Magnif. 950 ×.

number of ring-bivalents per P.M.C. varies between 1 and 3. Chiasmata are interstitial, subterminal or terminal. A hundred P.M.C's showed 0,82 ring-bivalents per cell and a frequency of $1{,}2 \pm 0{,}01$ chiasmata per bivalent. In 200 analysed P.M.C's 1 univalent was counted, the univalent frequency thus being only 0,5 %.

In this species secondary pairing occurs at first metaphase. Secondary pairing has been observed earlier in *C. neglecta* by FLOVIK (1938).

Calamagrostis arundinacea.

$2n = 28$, Figs. 7—15. Material: 3 plants from Härnösand, 5 plants from Sala and 2 from Järlåsa in Upland, 2 from Boxholm, 2 each from Åsljunga and Röstånga in Scania. All the other plants included in these examinations have been studied in acetocarmine.

The meiosis proceeds regularly in this species, though minor disturbances occur at times. Altogether 286 P.M.C's have been analysed. The combination 1 quadrivalent + 12 bivalents was found 21 times, 1 trivalent + 12 bivalents + 1 univalent three times, while the remaining 262 cells had 14 bivalents. One hundred P.M.C's showed on an average $1{,}3 \pm 0{,}01$ chiasmata per bivalent. The number of ring-bivalents amounted to 2,13 per P.M.C. For studies of the univalent frequency three plants were taken from Härnösand (H), Sala (S) and Röstånga (R). The last-mentioned had only bivalents in the reduction division. The two others had trivalents and quadrivalents in addition.

Number of univalents in C. arundinacea.

Field No.	No. of P.M.C's	No. of P.M.C's having 1 or 2 univalents
H 9—38	200	19
S 15—38	200	20
R 2—38 A	200	2
Total	600	41 = 6,8 %.

Measurements of the pollen from the 16 *C. arundinacea* plants from which pollen samples were taken in 1943 showed a mean value of 93,2 % morphologically good grains. Thus, 6,8 % aborted, which agrees with the 6,8 % of P.M.C's with univalents. Solitary plants with 29 chromosomes were obtained from *C. arundinacea*. Presumably, however, the supernumerary chromosomes originate from the female side.

Inversions occur sparingly in this species (Fig. 12). This has been

observed earlier by WESTERGAARD (1943) in *C. epigeios*. In my material only four had been observed after a study of 200 divisions. As in *C. varia* and *C. neglecta*, secondary pairing occurs.

C. arundinacea with fragments. — A plant obtained from Sörljusne in Hälsingland possessed one fragment. The fragment, which regularly lay at the outer edge of the plates at first metaphase, divided just as regularly at first anaphase and could also be traced in the second division.

Calamagrostis canescens.

$2n = 28$, Figs. 16—21. Material: 1 plant from Östersund, 2 from Källsta in Medelpad, 2 from Upsala, 3 from Eskilstuna, 1 from Kalmar, 2 each from Södra Rörum and Linderöd in Scania. All the other plants were examined in acetocarmine.

In rare cases a ring-quadrivalent occurs. Trivalents have not been observed. Of 200 analysed P.M.C's 197 exhibited 14 bivalents and 3 had 1 quadrivalent + 12 bivalents (the plant from Östersund). Examination of 100 P.M.C's gave an average of $1{,}4 \pm 0{,}01$ chiasmata per bivalent. The chiasmata are interstitial or terminal. Ring-bivalents occur to a number of 2,75 per P.M.C. with a maximum of four per cell. The mean univalent frequency was determined for three plants from Östersund, Upsala and Linderöd at 1,2 %.

Calamagrostis neglecta.

$2n = 28$, Figs. 22—27. Material: 12 plants from Burträsk in Västerbotten, 2 from Åmål in Dalsland, 1 from Gräsö in Upland. All the other *C. neglecta* plants were examined in acetocarmine.

The species has been examined by FLOVIK on material from Spitzbergen (1938, p. 279). He has established the occurrence of solitary quadrivalents in a relatively large number of cells (14). This has now been confirmed on Scandinavian material. As in FLOVIK's investigation, the quadrivalents found consisted of chains as well as rings, the latter being in the majority. This distribution was obtained within the same loculus of one plant from Åmål in 100 analysed P.M.C's:

Configuration	$1_{IV} + 12_{II}$	14_{II}
Number of P.M.C's	28	72

Of the 28 quadrivalents, 16 were rings and 12 chains. The above-mentioned loculus contained 0,28 quadrivalents per P.M.C. Analysis of 100 P.M.C's showed a chiasma frequency of $1{,}4 \pm 0{,}01$ per bivalent. On 200 P.M.C's the average possessing univalents worked out at 4,5 %.

At second metaphase and anaphase chromosomes are often eliminated, in addition to which an irregular division of the quadrivalents occurs. Not all pollen-grains will therefore contain 14 chromosomes. A few plants in the progeny from *C. neglecta* show aberrant numbers, 27, 29, 30 and 31. Presumably these numbers depend upon disturbances on the female side. FLOVIK's observation of secondary pairing has been confirmed.

Calamagrostis epigeios, 2n = 28.

Figs. 28—38. Material: 2 plants from each of the following localities: Järlåsa in Upland, Åmål in Dalsland, Strömstad in Bohuslän, Boxholm in Östergötland, Norra Ryd in Småland, and Gualöf, Tosterup, Röstånga, and Källstorp in Scania.

The species has been examined by WESTERGAARD (1943). He recorded a quite regular reduction division in four plants. The only distribution found was 14 bivalents.

Analyses of 250 P.M.C's gave the following results:

Distribution in 250 analysed P.M.C's from tetraploid C. epigeios.

Field No.	$4_{IV}+6_{II}$	$3_{IV}+8_{II}$	$2_{IV}+10_{II}$	$1_{IV}+12_{II}$	14_{II}
Järlåsa 1—41				2	23
Åmål 2—38 A	2	3	5	3	12
Strömstad 2—41 B				2	23
Boxholm 2—38		4	2	8	11
» 2—41 B		1		6	18
N. Ryd 1—41 A				1	24
Gualöf 2—41 B				1	24
Tosterup 1—41 B		2	1	4	18
Röstånga 1—38 A		1		3	21
Källstorp 1—39		1	3	2	19
Total	2	12	11	32	193

Grand total = 250.

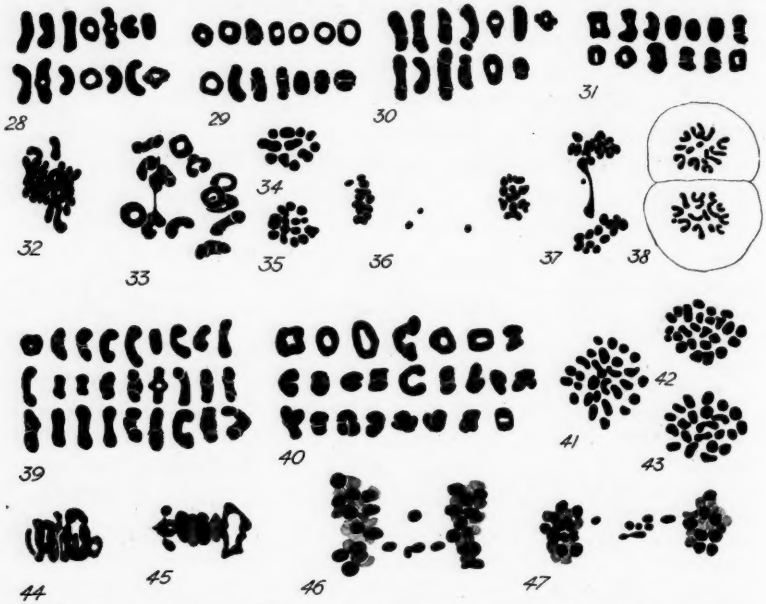
Thus, on an average 0,39 quadrivalents occurred per P.M.C. In most cases the quadrivalents were rings, rarely chains. Some of the rings were zigzag quadrivalents. Trivalents were found in 21 cases, though on no occasion more than one per P.M.C. The chiasmata are terminal or interstitial, subterminal ones occur sparingly. The chiasma frequency was determined in 250 P.M.C's and showed a mean value of $1{,}5 \pm 0{,}01$.

For evaluation of the univalent frequency plants were taken from Boxholm, Åmål, Röstånga and Källstorp.

Univalent frequency in tetraploid C. epigeios.

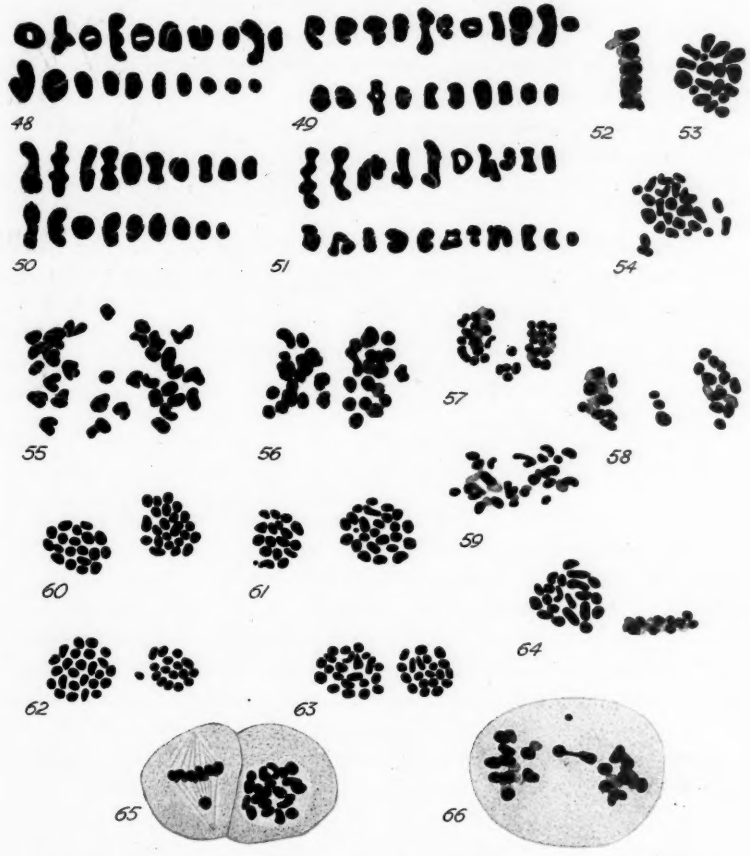
Field No.	No. of P.M.C's	No. of P.M.C's with 1—2 univalents
Boxholm 2—38	200	3
Åmål 2—38 A	200	3
Källstorp 1—39	200	4
Röstånga 1—38 A	200	2
B	200	2
C	200	2
Total	1,200	16 M = 1,3 %.

Division of the univalents at first anaphase was sometimes observed. The multivalents sometimes disunited at diakinesis. In one case it was



Figs. 28—47. *C. epigeios.* P.M.C's, meiosis. — 28—38, tetraploid. 28, 29, first metaphase with 14 bivalents. 30—31, first metaphase with 1 quadrivalent and 12 bivalents. 32, two quadrivalents and 10 bivalents. 33, the disjunction of a quadrivalent during first metaphase. 34, three quadrivalents and 8 bivalents. 35, two quadrivalents and 10 bivalents. 36, first anaphase with lagging chromosomes. 37, first anaphase with inversion bridge. 38, second metaphase with a fragment in the lower cell. — 39—47, octoploid. 39, first metaphase with 1 quadrivalent and 26 bivalents. 40, first metaphase with 4 quadrivalents and 20 bivalents. 41, first metaphase with 28 bivalents. 42, first metaphase with 3 quadrivalents and 22 bivalents. 43, first metaphase with 6 quadrivalents and 16 bivalents. 44—45, first metaphase with various hexavalents. 46, first anaphase. 47, first anaphase with lagging chromosomes. — Figs. 28—33, 39—40, 46, acetocarmine. — Magnif. 1040 ×.

observed that a quadrivalent disassociated before the chromosomes had yet had time to form a chromosome plate at first metaphase (Fig. 33).



Figs. 48—66. *C. epigeios,* hexaploid. P.M.C's, meiosis. — 48, first metaphase, probably with 2 quadrivalents, 4 trivalents, 8 bivalents and 6 univalents. 49, first metaphase, probably 5 trivalents, 11 bivalents and 5 univalents. 50, first metaphase, probably 2 quadrivalents, 3 trivalents, 11 bivalents and 3 univalents. 51, first metaphase with 1 quadrivalent, 3 trivalents, 14 bivalents and 3 univalents. 52, first metaphase with 21 bivalents. 53, first metaphase, probably 3 quadrivalents, 3 trivalents, 9 bivalents and 3 univalents. 54, first metaphase, perhaps 1 trivalent, 16 bivalents and 7 univalents. 55—59, first anaphase. 60—64, second metaphase. 60, distribution 19—23; 61, 17 1/2—24 1/2; 62, 25—1—16; 63, 22—20; 64, 21—21. 65, second metaphase. 66, first anaphase with inversion bridge. — Figs. 48—51, 55—56, aceto-carmine. — Magnif. 1080 ×.

Inversions were sparing in occurrence; only four were found with certainty at first anaphase.

Calamagrostis epigeios, 2n = 42.

Figs. 48—66. Material: 3 plants from Lycksele in Lapland, 1 from Vansbro in Darlecarlia, 1 from Strömstad in Bohuslän and 1 from Boxholm in Östergötland.

Hexaploid *C. epigeios* seems to occur principally as a hybrid between tetraploid and octoploid *C. epigeios*. It hardly occurs as an independent race, even if it can form complexes by vegetative propagation.

The type exhibits the greatest variation of all amphimictic species. Analysis of the P.M.C's is often difficult, and therefore it has only been possible to examine 51 of them.

Configurations found in hexaploid C. epigeios.

Configurations							No. of P.M.C's
VI	V	IV	III	II	I		
1	—	4	—	9	2		1
1	—	3	1	9	3		2
1	—	2	—	13	2		2
1	—	1	—	14	4		1
1	—	—	—	18	—		1
—	1	4	2	6	3		2
—	1	4	—	10	1		1
—	1	1	—	16	1		1
—	—	5	—	6	10		1
—	—	4	3	6	5		1
—	—	4	1	10	3		3
—	—	3	3	9	3		2
—	—	3	2	11	2		3
—	—	3	1	13	1		6
—	—	2	5	7	5		1
—	—	2	4	8	6		2
—	—	2	3	11	3		1
—	—	2	2	13	2		2
—	—	2	1	14	3		1
—	—	2	—	14	6		1
—	—	1	3	13	3		1
—	—	1	1	17	1		7
—	—	—	5	11	5		1
—	—	—	1	19	1		1
—	—	—	1	16	7		1
—	—	—	1	14	11		1
—	—	—	—	21	—	(Fig. 52)	1
—	—	—	—	20	2		3

In the 51 analysed P.M.C's the hexavalents numbered 7, pentavalents 4, quadrivalents 106, trivalents 69, bivalents 655 and univalents 137, giving the following mean values per P.M.C.:

Hexavalents	0,14	Pentavalents	0,08
Quadrivalents	2,08	Trivalents	1,35
Bivalents	12,84	Univalents	2,69

The chiasma frequency was determined in 250 P.M.C's and showed a mean of $1{,}5 \pm 0{,}02$ chiasmata per bivalent.

A calculation of the univalent frequency on 4 plants gave the following result:

Univalent frequency in hexaploid C. epigeios.

Field No.	No of P.M.C's	No. of univalents per P.M.C. 0	1	2	3	4	5	6	7	8	9	10
Lycksele 1—38 ..	200	6	11	32	34	31	28	26	18	6	6	2
» 2—38 ..	200	16	15	32	35	43	30	17	5	4	3	
» 3—38 ..	210	16	7	23	50	27	32	24	20	6	3	2
Boxholm 1—41 B	100	11	19	27	28	7	3	4	1			
Total	710	49	52	114	147	108	93	71	44	16	12	4

The mean number of univalents per P.M.C. works out at $3{,}7 \pm 0{,}68$. This corresponds fairly well with the figure for the analysed plates, or 2,69. In consequence of the fairly large number of univalents eliminated during meiosis, as well as the irregular distribution of multivalent derivatives, the fully developed pollen-grains contain varying numbers. All numbers between 16 and 25 (second metaphase) were directly observable under the microscope. Theoretically, therefore, the progeny ought to have chromosome numbers varying between 32 and 50, provided similar disturbances occur on the female side and no allowance is made for unreduced gametes. This question is illuminated later on by the crossing results.

Lagging chromosomes are common at first as well as at second anaphase, as is to be seen from the figures. On the other hand, pollen-grains with distinct micronuclei are rare. There is much variation in pollen-grain size, and unreduced gones are therefore probably common on the male side. Sometimes the shape of the pollen-grain also varies.

Calamagrostis epigeios, $2n = 56$.

Figs. 39—47. Material: 5 plants from Härnösand, 1 from Östersund and 2 from respectively Landskrona and Gualöf in Scania. All the other plants analysed were examined in acetocarmine.

This type has been examined earlier by WESTERGAARD (1943). All the P.M.C's studied in his material contained quadrivalents to a number of 1—5.

WESTERGAARD's find of quadrivalents has been confirmed in the present material. In rare cases hexavalents also occur. Sixty P.M.C's have been analysed.

Configurations found in octoploid Calamagrostis epigeios.

Field No.	Configuration VI	IV	III	II	I	No. of. P.M.C's
H—ep	1			25		2
	1	1		23		1
		6		16		1
H 6—38				28		10
		1		26		2
		2		24		1
H 8—38 A	1	1		23		1
	1	2		21		1
				28		2
		1		26		1
		2		24		2
		3		22		4
		4		20		2
		5		18		1
B				28		2
		1		26		1
		2		24		1
C		2		24		1
		1	2	22	2	1
		2	1	22	1	1
Gualöf 1—41				28		1
		1		26		2
		2		24		1
		3		22		1
L—a 1—41				28		1
		1		26		2
		2		24		1
		3		22		1
Ö—d J 3—38	1	1		23		1
	1	2		21		1
				28		1
		1		26		2
		2		24		3
		5		18		1
		1	1	24	1	2
		2	1	22	1	1

The number of hexavalents per P.M.C. is 0,12, quadrivalents 1,33 and trivalents 0,10. In solitary plants, however, there is a higher frequency of hexavalents. For instance, in plant H-ep 8 hexavalents were counted in a loculus of 51 cells, many of which, however, could not be analysed in their entirety. The combination 28_{II}, which WESTERGAARD did not find in his material, occurred here in fully one-fourth of all analysed P.M.C's (28,3 %).

The univalent frequency was determined on 5 plants from Härnösand and 1 from Östersund (J 3—38).

Univalent frequency of octoploid Calamagrostis epigeios.

Field No.	No. of P.M.C's	No. of P.M.C's having number of univalents given below		
		1	2	3
H—ep	200	11	4	1
H—p	200	14	3	
H 1—38 B	100	3		
H 8—38 A	100	9	2	1
B	100	4		
J 3—38	100	5		
Total	800	46	9	2

Mean univalents per P. M. C. = 8,75 %.

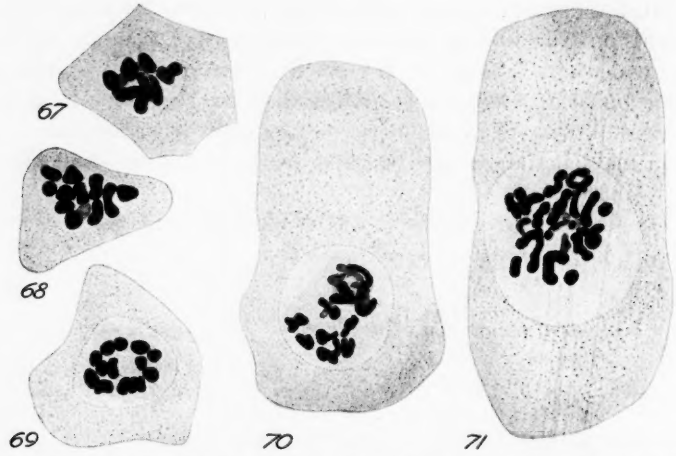
The chiasma frequency was determined on 60 cells. The mean was 1,4 ± 0,02 chiasmata per bivalent.

As a rule the anaphase follows a normal course, though now and then lagging chromosomes appear. Split univalents were observed in some cases. At times whole bivalents pass undivided to one of the poles. This was observed several times in different species within the genus. Presumably it is due to irregularities in the spindle. Such are common in the apomictic species.

Inversions have been observed by WESTERGAARD in this karyotype. He states that bridge formations are common. In the present material only two undoubted cases were found, both at first anaphase.

b. The female side.

E.M.C's were examined in all amphimictic species. They were often difficult to analyse, however, and only a few could be completely studied (Figs. 67—71).



Figs. 67—71. Meiosis in E.M.C's of amphimictic species. — 67, *C. varia*, first metaphase with 14 bivalents. 68, *C. neglecta*, first metaphase with 2 quadrivalents and 10 bivalents. 69, *C. arundinacea*, first metaphase with 14 bivalents. 70, *C. epigeios* ($2n = 28$), 14 bivalents, diakinesis. 71, *C. epigeios* ($2n = 42$), pro-metaphase, probably with 3 trivalents, 16 bivalents and 1 univalent. — Magnif. 1430 ×.

Analysis of E.M.C's in amphimictic Calamagrostis species.

Species	No. of E.M.C's	Configuration
C. varia	2	14_{II}
arundinacea	10	14_{II}
canescens	6	14_{II}
neglecta	5	14_{II} (4), $2_{IV} + 10_{II}$ (1)
epigeios $2n = 28$	2	14_{II}
$2n = 42$	2	$3_{III} + 16_{II} + 1_{I}$, $1_{III} + 19_{II} + 1_{I}$
$2n = 56$	0 fully analysed	VI's and IV's occur

The E.M.C's behave on the whole like the P.M.C's. Considerable disturbances seem only to occur in hexaploid *C. epigeios*. In addition it would appear from the crossing results for *C. neglecta* and octoploid *C. epigeios* that E.M.C's with other numbers than the halved also function at the formation of embryo-sacs.

The amphimictic *Calamagrostis* species previously referred to show a *regular meiosis as tetraploids, a disturbed meiosis as octoploids, and an irregular meiosis as hexaploids.* This rule also applies to the Central-European species *C. pseudophragmites*, *C. tenella* and *C. villosa*, which are all amphimictic species.

B. THE BREAK-DOWN OF MEIOSIS IN APOMICTIC SPECIES.

a. Terminology.

The apomictic *Calamagrostis* species possess many types of division. To describe these the terms recommended in works by ROSENBERG (1917, 1926—27) and EDMAN (1931) have been adopted. A conspectus of the terminology has been given by GUSTAFSSON (1944).

b. Pollen mother cells.

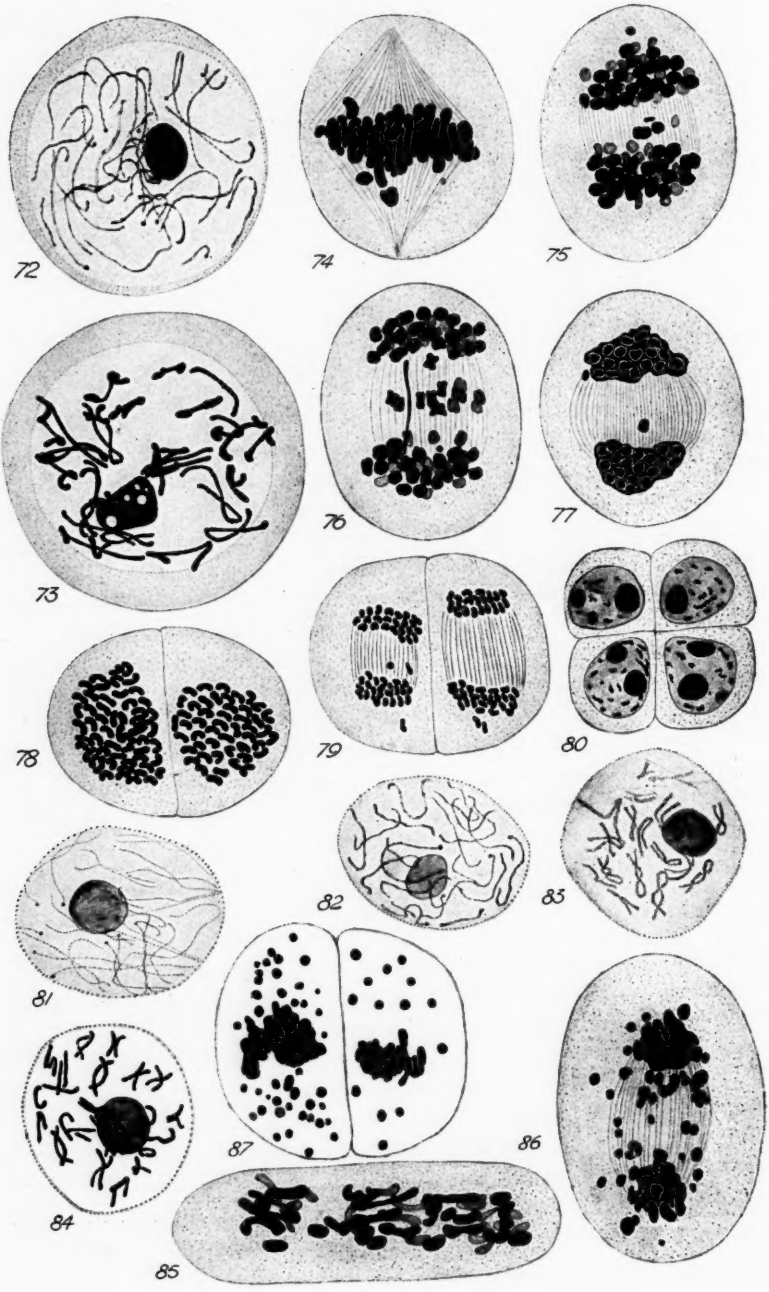
Calamagrostis lapponica.

Chromosome numbers: $2n = 42$—112. Material: All the 57 plants included in the investigation have been examined in acetocarmine. Of these, 28 were studied after cutting embedded material. They have the chromosome numbers 49, 98, 102, 103, 105, 107 and 112. The plants are derived from different parts of Lapland. They were fixed in nature, four in the experimental fields at Svalöf.

As already pointed out in the introduction, no pollen is formed as a rule in this species. In 11 of the 28 examined plants, however, it was possible to find pollen. Only rarely is pollen formed in all the loculi of an anther, usually merely in a part of the loculus. The fact is that the P.M.C's generally degenerate at an early stage. This degeneration may proceed in several different ways, and at times it befalls pollen, pollen tetrads, and even P.M.C's in process of division. The degeneration is often combined with formation of polyads and plasmodia.

Scheme showing behaviour of the P.M.C's in Calamagrostis lapponica.

I. *Divisions occur.*
  A. P.M.C's free.
    1. Meiosis.
      (a) Normal. Univalents 0—10 per P.M.C.
      (b) As preceding. Above 10 univalents per P.M.C.
      (c) Abnormal. P.M.C's elongated, chromosomes scattered.
      (d) Pre-meiotic disturbances cause P.M.C's to have double the chromosome number.
      (e) c and d in combination with formation of restitution nuclei give P.M.C's having the chromosome numbers n—$8n$.
    2. As yet unelucidated type of division with chromosomes of mitotic appearance.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B. Plasmodia.
(a) Formed from P.M.C's the walls of which disintegrate before meiosis sets in. The nuclei can pass through all phases of meiosis. Formation of restitution nuclei gives rise to giant nuclei in the plasmodia.
(b) Formed during or after meiosis.

II. *No divisions.*
A. Resting cells. The nuclei of the P.M.C's remain in the resting stage. All P.M.C's degenerate. The commonest type.
B. Plasmodia. Formed from P.M.C's whose walls have disappeared.

Normal meiosis, with only minor disturbances in the form of 0—10 univalents per P.M.C., occurred only in a plant from Abisko in Lapland. Re-examinations one year later of the population to which the plant belonged showed that its members could produce up to 78 % of morphologically good pollen.

Strangely enough, just the above-mentioned plant had no E.M.C's with a meiotic type of division. However, meiosis occurs in the E.M.C's of other plants in the same population. Figs. 72—80 show the division in the P.M.C's.

Nine of the examined plants possessed P.M.C's containing more than 10 univalents and a well-developed spindle. Even this type can produce pollen without micronuclei.

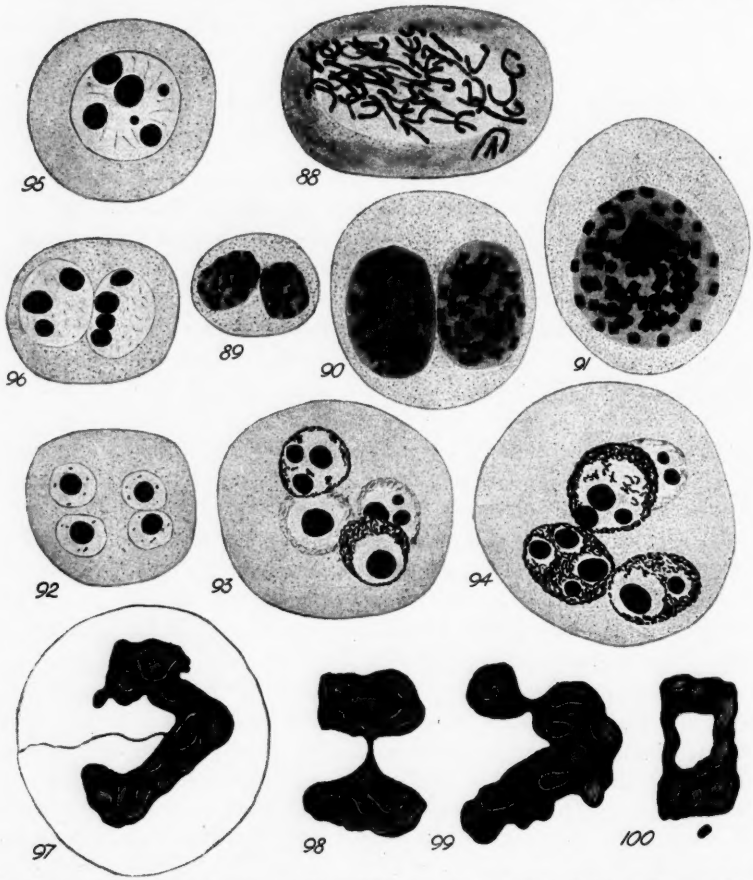
The reduction division was abnormal in all the 11 plants with pollen except the individual mentioned above from Abisko. Presumably the irregularities are due to disturbances in the function of the spindle. It was possible to study this division type thoroughly in six plants from Abisko and Porjus in Lapland.

One plant with the chromosome number $2n = 49$ from Porjus also possessed earlier prophase stages that were analysable. It was found that pairing occurred at zygotene, but as a rule no chiasmata were formed and hence the pairs disassociated in the course of meiosis. At times they persisted right up to diakinesis; usually they disunited at late diplotene (Figs. 81—84). During first metaphase the chromosomes are distributed at random in the P.M.C's (Fig. 85). Univalents, bivalents

Figs. 72—87. *C. lapponica.* P.M.C's. 72—80, normal meiosis. — 72, pachytene. 73, diplotene. 74, first metaphase. 75, first anaphase. 76, first anaphase with inversion bridge. 77, first telophase. 78, second metaphase. 79, second anaphase. 80, tetrad. — 81—87, meiosis disturbed. 81, zygotene. 82, pachytene. 83, early and 84 late diplotene. 85, »first metaphase». 86, fragmented chromosomes at first anaphase—telophase. 87, the same in second metaphase. — Magnif. 1300 ×.

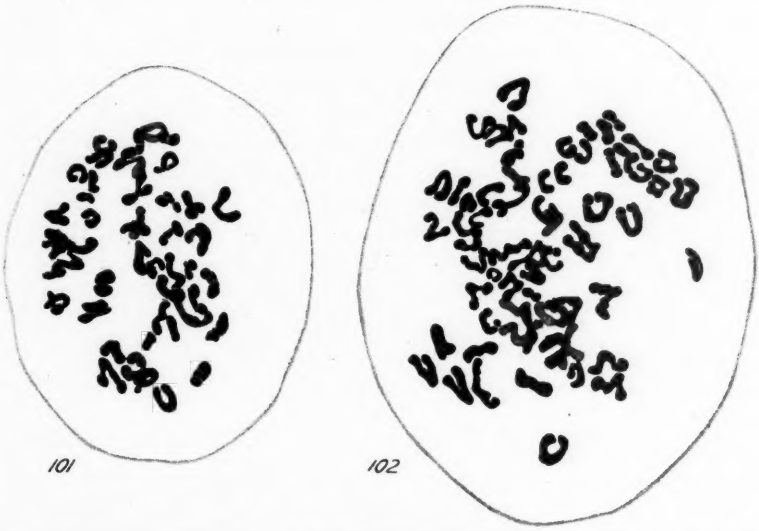
and also higher units lie in hopeless confusion. Sometimes the chromosomes are associated in groups in the P.M.C's (Fig. 109). In each group they afterwards divide, and the final product will be a multinucleate giant-cell that resembles the plasmodia.

Chromosome fragmentation sometimes takes place in the P.M.C's.



Figs. 88—100. *C. lapponica* ($2n = 49$). P.M.C's. — 88, »mitotic» division. 89, nuclei in interkinesis, probably with altogether 49 chromosomes. 90, nuclei in interkinesis with altogether 196 chromosomes. 91, nucleus in interkinesis with 196 chromosomes. 92, tetrad, each nucleus has the haploid chromosome number. 93, the same with the diploid number. 94, the same with the tetraploid number. 95, pollen grain, probably with the tetraploid chromosome number. 96, dyad, each nucleus with the diploid chromosome number. 97—100, restitution nuclei. — Magnif. 1100 ×.

It may proceed in different stages. Usually bivalents and higher units seem to get along the best, while the univalents split into very small bits. If the fragmentation is combined with failure of wall formation at first telophase, complete chaos arises in the P.M.C. (Fig. 104). Similar disturbances have been previously described, among others by HOLMGREN in *Eupatorium glandulosum* (1919) and by GENTCHEFF and GUSTAFSSON in *Hieracium robustum* (1940). At times bent and twisted



Figs. 101—102. *C. lapponica.* P.M.C's from the same anther. — 101, with the chromosome number $2n$ (= 112). 102, a syndiploid cell with the chromosome number $4n$ (= 224). Acetocarmine. — Magnif. 1000 ×.

spindles arise (Fig. 103). Abnormalities of this kind have been observed on several earlier occasions (TISCHLER, 1943, pp. 619—620).

If the walls between adjoining P.M.C's are disintegrated, plasmodia of a very complex appearance are formed. In Fig. 107 a plasmodium of this kind is seen in which chromosomes from several P.M.C's lie planlessly strewn in the large cell. In such cases chromosome associations of a higher order seem able to arise. The large arched chromosome at the bottom of the picture consists of at least ten units. Other types of this sort of plasmodium are seen in Figs. 106 and 108. In Fig. 106 a large number of chromosomes are scattered in the cell; in Fig. 108 they have divided into groups and formed telophase plates and

restitution nuclei. Fig. 112 may be regarded as a final stage in such plasmodial formations. The nuclei are of very variable size.

Pre-meiotic associations of P.M.C's have been observed in two plants. In Figs. 101 and 102 a cell is seen of the type $2n$ and another of the type $4n$. The cells are derived from the same anther (aceto-carmine preparation). In this case it was possible to ascertain that multivalent formation was better established in the cell with the number $4n$ than in that of the $2n$ type. The association had therefore probably taken place at a very early stage.

In *C. lapponica* restitution nuclei are formed. Frequently syndiploidy also occurs. These phenomena may be combined at times, in which case high chromosome numbers are formed in the cells. Restitution nuclei in ROSENBERG's sense are illustrated in Figs. 97—100. The three P.M.C's in Figs. 89—91 are all derived from the same loculus. In Fig. 89 the two nuclei together may contain 49 chromosomes ($2n$), in Fig. 90 each of the nuclei contains 98 ($4n$), and in Fig. 91, 196, i. e. $8n$. The tetrads in Figs. 92, 93 and 94 have the numbers n, $2n$ and $4n$ respectively in each nucleus. Giant pollen grains, to all appearances $4n$, are seen in Fig. 95. Whether such pollen is germinable is difficult to ascertain. Similar observations on other material have been made by GENTCHEFF (1937, p. 177), SAKAMURA and STOW (1926) as well as STRAUB (1939, p. 444).

Fig. 88 shows an interesting type of division that only occurs in the plant ($2n = 49$) from Porjus. It occurs very sparingly, having only been found in eight loculi, and deviates from all observed types of division in *Calamagrostis*. The chromosomes are long and slender as in a mitosis. The figure shows the type most common. In other P.M.C's the contraction of the chromosomes varies very much. No equatorial plate has ever been discovered, the chromosomes lying planlessly scattered in the same manner as the univalents lie in the semiheterotypic division of the *Hieracium laevigatum* scheme (ROSENBERG, 1917, 1926—27). Later stages have not been observed.

Plasmodia of type II B or resting cells that never undergo division occur in all *C. lapponica* plants, except in the one with a regular reduction division from Abisko. Later stages of this, however, are missing. Other plants belonging to the same population possess plasmodia or resting cells. In some plants the number of florets having plasmodia, resting cells and some type of reduction division has been determined. The frequency varies much in different plants, as can be seen from the following table.

Table showing frequency of florets with reduction division, plasmodia or resting cells in Calamagrostis lapponica.

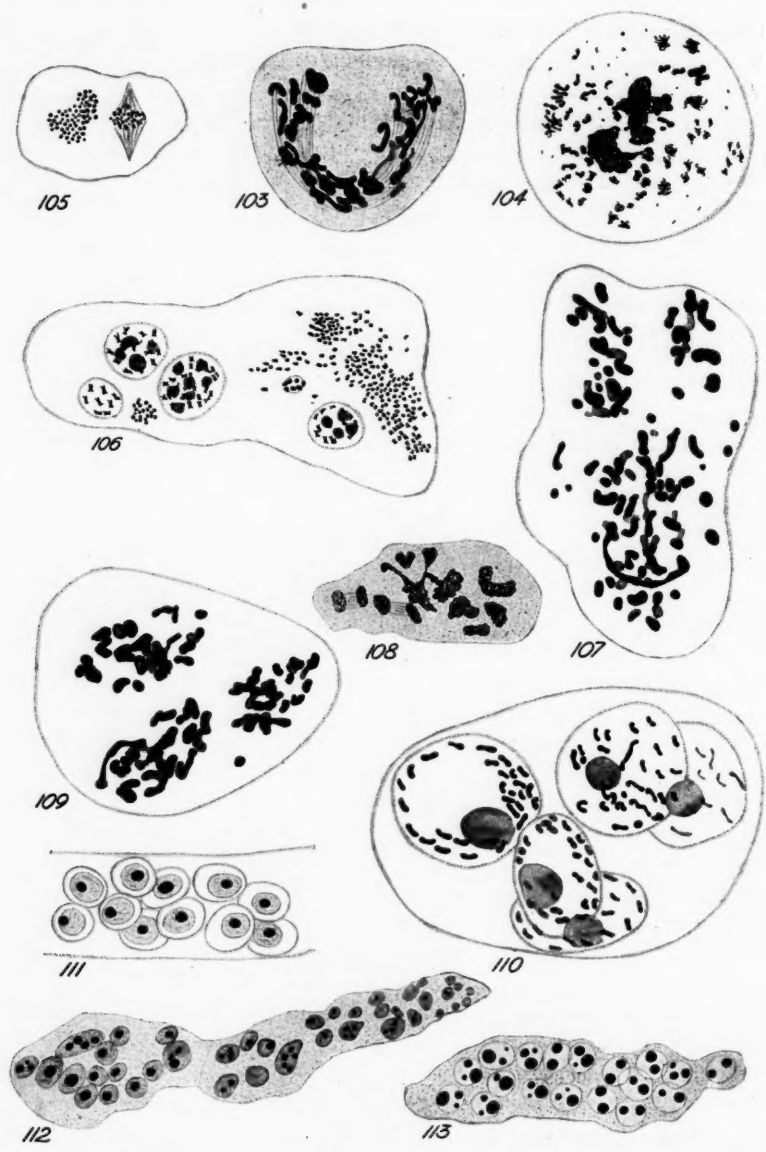
No.	Place of origin	Total No. of florets	Meiosis		Resting cells		Plasmodia	
			No. of fl.	%	No. of fl.	%	No. of fl.	%
1549—50	Porjus	395	129	32,7	161	40,8	272	68,9
1551—52	Porjus	118	84	71,2	5	4,2	71	60,2
1553	Porjus	211	0	0	162	76,8	138	65,4
1573	Abisko	103	68	66,0	7	6,7	72	69,9
1577	Abisko	93	60	64,5	35	37,6	20	21,5
1595	Adnetjocko, 1100 m. s. m.	57	0	0	0	0	57	100

It will be seen from the above table that P.M.C's in meiosis, resting cells as well as plasmodia may occur in the same floret, even in the same loculus of an anther. No general rule to indicate where the disturbances in a loculus are greatest can be given on account of the enormous changes from loculus to loculus and from plant to plant. None the less, it seems to me that the more regular stages are usually to be found in the middle of the loculus, while grosser disturbances or more numerous plasmodia and resting cells occur towards the ends.

On going over the *C. lapponica* material one is surprised by the lack of normal stages. Only one of the examined plants possesses the property of regularly forming pollen without micronuclei. The disturbances are very variable even within the same loculus. They are in many respects reminiscent of disturbances known from material treated with narcotics, colchicine or similar poisons, plants exposed to the attacks of parasites or suffering from deficiency diseases (cf. TISCHLER, 1943). Most striking, however, is their likeness to the effect of extreme temperatures (STRAUB, 1939). Drought can sometimes act in the same way (STRAUB, 1936; OEHLKERS, 1937; H. ERNST, 1938). The sovereign nonchalance of the species to formation of pollen tetrads is striking. The successive type changes to the simultaneous one. In addition, wall formation is often abolished, plasmodia being then formed.

A calculation of the frequency of the division types in *C. lapponica* from Porjus disclosed that in one and the same loculus 65 P.M.C's had undergone the successive and 49 the simultaneous division. At the same time two restitution nuclei were observed at first telophase.

The irregularities that occur are, however, too often represented in the species to be caused solely by external conditions. Most probably, the many disturbances have genetic causes. Some support for this has



Figs. 103—113. *C. lapponica.* P.M.C's. — 103, turned spindle. 104, fragmentation at first telophase. 105, plasmodium with two nuclei and chromosomes in division.

been obtained from an examination of the progeny of an isolated plant from Lycksele. Nine daughter-plants showed the same disturbances in the meiotic mechanism as their female parent. Regular meiosis in the P.M.C's is extremely rare and to all appearances does not occur in the E.M.C's. One plant with a regular meiosis in the P.M.C's had no meiosis in the E.M.C's. Another plant showed weak disturbances in the E.M.C's but much stronger ones in the P.M.C's (cf. GUSTAFSSON, 1938).

The great disturbances in the plant from Porjus were probably due to an interaction of internal and external factors. During the nights just preceding its fixation there was a very strong frost for the time of year (end of July, 1944, — 5° C.). The plant, which on account of its genotypic constitution was already liable to exhibit an irregular meiosis, over and beyond this received a severe cold shock just at the time the prophase was starting in the young florets. This shock also involved disturbances in the development of the E.M.C's (see p. 171). From STRAUB's examinations of *Gasteria trigona* (1939) it is known that a hot shock during the pachytene stage results in a total failure of chiasmata. Other results show that low temperatures can have the same effect (*Rhoeo discolor*; STRAUB, 1936). It may therefore be assumed that the influence of low temperatures in plants with a more or less genetically controlled failure of the meiosis contributes to increasing the extent of the disturbances.

Of great interest in this connexion is the increase in the number of chromosomes that can occur in P.M.C's and E.M.C's. In no single case, however, has pollen been obtained from plants that have been fixed in the alpine regions of the Swedish mountains. Four such plants have been examined. They were all from localities situated more than 1.000 metres above sea-level. All show plasmodium formation. In the localities where these plants grow the temperature drops practically every night down to or below 0° C. during the period of vegetation. These repeated cold shocks probably inhibit the development of the P.M.C's. The plants have not flowered at Svalöf and therefore nothing can be said regarding their behaviour in a milder climate.

If cold shocks are able to modify the development in the P.M.C's in *C. lapponica*, the peculiar mitotisized type of division (I A: 2, p. 147)

106, giant-plasmodium with chromosomes in interkinesis. 107, plasmodium, chromosomes in first metaphase. 108, plasmodium with many nuclei, some in telophase. 109, the formation of a plasmodium, the chromosomes in groups in the cell. 110, plasmodium with five nuclei. 111, »resting cells». 112, plasmodium, the nuclei of different size. 113, plasmodium with nuclei of equal size. — Magnif. 990 ×; 105, 106, 108, 111—113 = 400 ×.

is perhaps to be interpreted as a form of mitosis. As a matter of fact, a case of this kind is known from similar material, viz. *Hieracium robustum* (GUSTAFSSON and NYGREN, 1946). In this case the temperature was so low in certain years that plants cultivated in the open only exhibited mitosis in the P.M.C's, while the specimens grown in greenhouses showed meiosis. The climate in the South of Scandinavia is not suitable for this South-European species.

Calamagrostis purpurea.

Chromosome numbers: $2n = 56$—91. Material: All the 174 plants included in the investigation were examined in acetocarmine. 119 plants with the chromosome numbers 56, 63, 70, 77 and 91 were examined in sectioned material, in certain cases very thoroughly. The plants were derived from various parts of Sweden (see p. 132). Most of them were fixed in nature, but a large number of plants were fixed at Svalöf. No noteworthy difference was observed between these fixations.

As can be seen from the synoptical table on page 133, no pollen was formed in the present material of this species. However, in 1941 the writer obtained from Gällivare in Lapland a plant that developed a certain amount of pollen. In spite of extensive personal investigations during the summers of 1944 and 1945 among natural populations in large parts of northern Sweden all attempts to obtain another plant of this kind proved unsuccessful. Two plants having the chromosome number 56 from Jormlien in north-western Jämtland show, however, divisions of the P.M.C's in a couple of loculi.

As in *C. lapponica*, varying types of division are encountered. The following have so far been discovered.

Scheme showing divisions in Calamagrostis purpurea.

I. *Divisions occur.*
  A. P.M.C's free.
    1. Meiosis.
      (a) Bivalents occur: *Hieracium boreale* scheme (ROSENBERG, 1917).
      (b) Bivalents absent: *Hieracium laevigatum* scheme (ROSENBERG, 1917). Semiheterotypic division (ROSENBERG, 1926—1927).
    2.
      (c) Intermediate division type. Reminiscent of *Hieracium pseudoillyricum* scheme (ROSENBERG, 1917) and *Hieracium echioides* (GENTCHEFF, 1937, p. 180).
    3. Mitosis.
      (d) Chromosomes purely mitotic. Very varying contraction. Retarded (BERGMAN, 1935 a, p. 226).

B. Plasmodia.

1. Pre-meiotic.
   (a) Divisions proceed as in free P.M.C's. Giant cells formed as in *C. lapponica.*
   (b) Nuclei exhibit diakinesis-like stages. Further divisions do not occur. Degenerate.
2. Formed during meiosis or mitosis.
   (c) Walls of P.M.C's disintegrate. The same plasmodium may exhibit plates with unequally contracted chromosomes.

II. *No divisions.*

A. P.M.C's free. The P.M.C's swell in size. They gradually lie free in the loculus. Sometimes a nuclear division may begin; such divisions are never completed. Degenerate.

B. P.M.C's united into plasmodia. The P.M.C. walls are disintegrated and form plasmodia, which may contain over 50 nuclei. Now and then the nuclei divide as if by chance in diakinesis-like stages, type I: B: 1: b then arising. Degenerate.

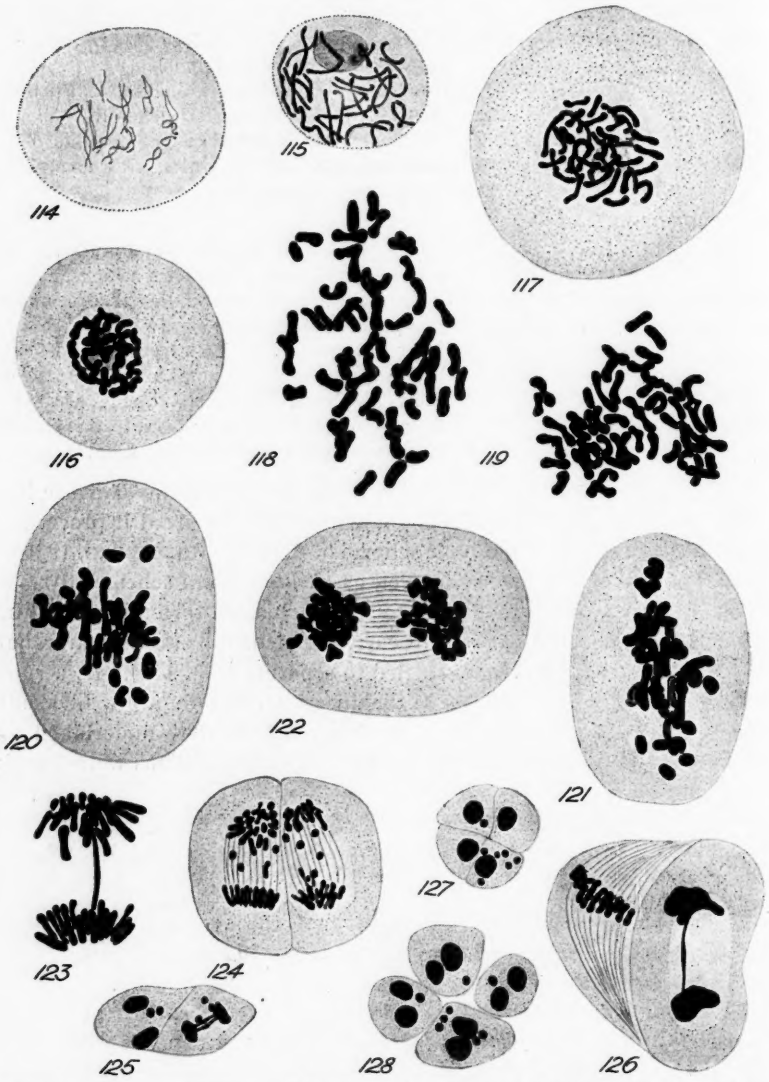
The pollen-bearing *C. purpurea* plant obtained from Gällivare has been very thoroughly examined. When meiosis occurred it proceeded according to the semiheterotypic scheme of division (ROSENBERG, 1926—27). The *Hieracium boreale* as well as *H. laevigatum* scheme (ROSENBERG, 1917) was represented. At zygotene chiasma formation could be demonstrated in certain cases. At early diplotene the chromosomes that had not developed chiasmata started to separate (Fig. 114). As a rule, this separation was completed in diakinesis, when only a few bivalents per P.M.C. were usually left. Complete analyses were undertaken on 50 cells at first metaphase and the following configurations were found:

Number of bivalents per P.M.C. in Calamagrostis purpurea.

No. of bivalents ..	0	1	2	3	4	5	6	7	8	9	10	11	12	13
No. of P.M.C's ..	14	6	5	4	6	2	3	3	2	1	1	1	1	1

The above-mentioned cells were analysed in one and the same anther in acetocarmine preparation. In sectioned material, however, up to 19 bivalents were found.

A more searching examination of the plant revealed that the *boreale* and *laevigatum* schemes were represented in some panicles with about the same frequency, while the frequencies in others were distinctly different. Which type dominates does not, to all appearances, depend on chance but on the age of the panicles and presumably also on certain external factors such as moisture and temperature during the time the panicles are being laid down (p. 183). The same panicle may also



Figs. 114—128. *C. purpurea.* P.M.C's. — 114, early and 115 late diplotene. 116—117, diakinesis with unequally contracted chromosomes. 118—121, first metaphase, 118, 56 univalents, 120—121 with »unequal bivalents». 122, first anaphase with regular distribution. 123, first anaphase with inversion bridge. 124, second anaphase with lagging univalents. 125—126, second telophase with inversion bridges. 127—128, tetrads of different size. — Figs. 118—119 and 123, acetocarmine. — Magnif. 1100 ×; 125, 127, 128 = 550 ×.

exhibit different values. This was known earlier from *Hieracium* as a result of ROSENBERG's investigations. A panicle that on being fixed separated into an upper older part (269) and a lower younger one (270) gave the following values for the two types:

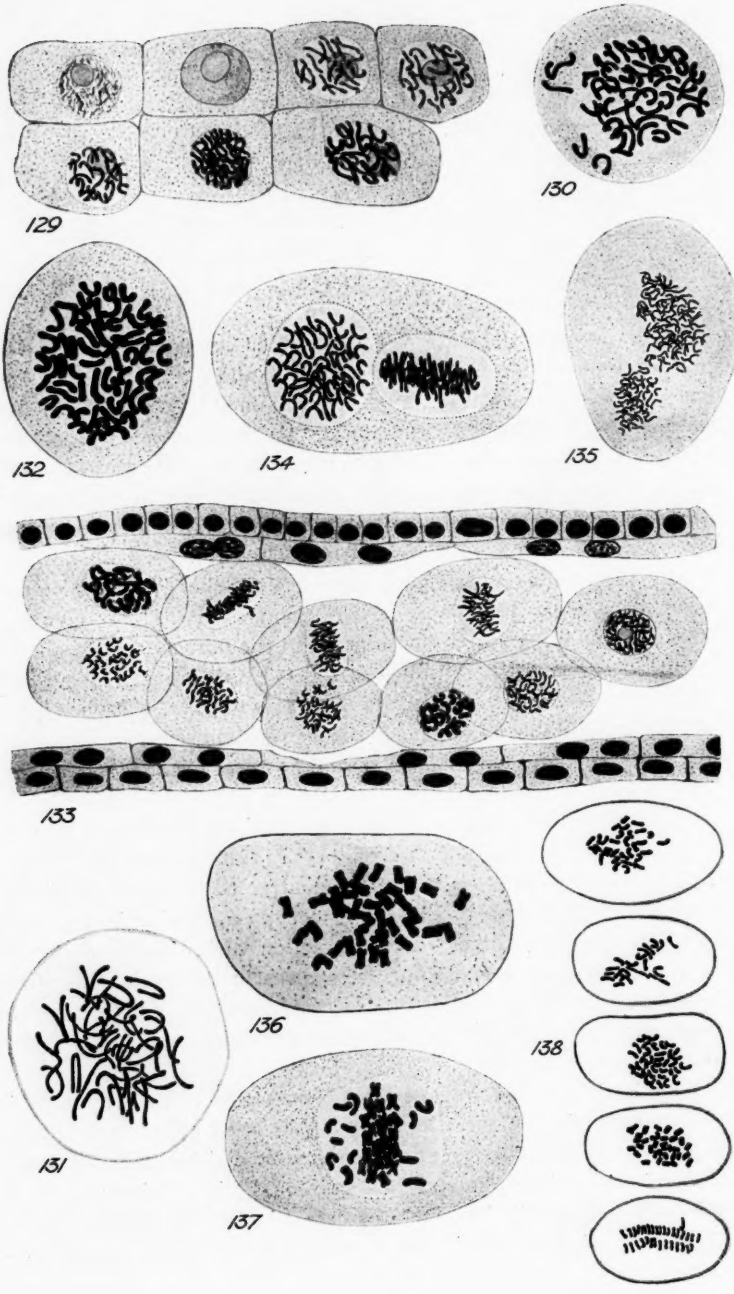
Fix. No.	*boreale* scheme		*laevigatum* scheme		No. of P.M.C's
270	409	81,2 %	95	18,8 %	504
269	183	56,5 »	140	43,5 »	324

Division according to the *boreale* scheme in *C. purpurea* often gives unequal bivalents at first metaphase (Figs. 120 and 121). The percentage of inversions is higher than in any other examined species of the genus. Bridge formations occur at first as well as at second division (Figs. 123, 125, 126). P.M.C's of the *boreale* scheme apparently undergo both divisions. The pollen formed is at times very rich in micronuclei. Division according to the *laevigatum* scheme terminates in dyads, which subsequently degenerate (cf. ROSENBERG, 1926—27).

In the *boreale* as well as the *laevigatum* scheme the univalents seem to pass each to its pole at first division. One or two, however, sometimes divide there and are eliminated in the *boreale* scheme during the second division. Where pollen is formed, this is surprisingly uniform. Its variation in size is considerably less than in, e. g., hexaploid *C. epigeios*. Both the *boreale* and the *laevigatum* scheme sometimes give rise to restitution nuclei. Such do not however occur by any means so often as in *C. lapponica*.

A type of division that in much resembles the *Hieracium pseudo-illyricum* scheme (ROSENBERG, 1917) occurs in some florets (Figs. 136—138). The chromosomes are rather too contracted to be called mitotic. They are distinctly doubled and seem to occupy a position intermediate between mitotic and meiotic. The contraction varies in different cells. The chromosomes do not arrange themselves in equatorial plates but lie scattered in the cell. Similar intermediate forms have been observed by GENTCHEFF (1937, p. 180) in *Hieracium echioides* and by FAGERLIND (1940, p. 31) in *Wikstroemia*.

The mitotic type of division in *C. purpurea* always appears in P.M.C's that remain in the resting stage, while other cells in the loculus, the anther or the floret have undergone meiotic division. Hence, sometimes loculi containing solitary P.M.C's with mitotic division are found, sometimes whole loculi. The last-mentioned is the commoner. Only a small fraction of these previously undivided P.M.C's undergo division,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however. The great majority degenerate, as occurs in all other examined *C. purpurea* plants. The mitotic type of division in *C. purpurea* corresponds most closely to the conditions described by BERGMAN (1935 a, p. 226) for *Leontodon hispidus*. Similar divisions are known from several *Hieracium* species (GUSTAFSSON, 1935, 1939; GENTCHEFF, 1937, 1941). In *Hieracium*, however, the mitotic type of division is earlier than the meiotic, while in *C. purpurea* it always occurs in delayed P.M.C's. The contraction of the chromosomes varies in a very high degree (Fig. 133).

The mitotic type of division is preceded by a swelling of the P.M.C. and more especially of the nucleus. This is a well-known fact from the mitotic type in E.M.C's (STEBBINS, BERGMAN, GUSTAFSSON). Measurements were made of nuclei belonging to meiotic and mitotic types in the same anther. The results are given in the following table:

Measurements of nuclei belonging to meiotic and mitotic types in P.M.C's of Calamagrostis purpurea.

Division type	Smallest nucl. found	Largest nucl. found	Mean	No. of cells
Meiosis	205 units	373 units	330 ± 11	35
Mitosis	733 units	2949 units	1569 ± 115	35
			t = 10,725	

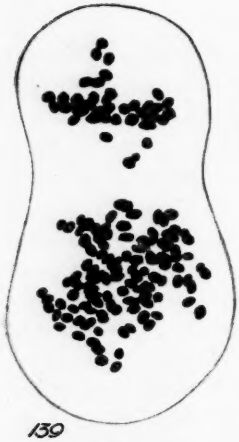
For the cells the following values were obtained:

Measurements of P.M.C's of C. purpurea belonging to meiotic and mitotic types respectively.

Division type	Smallest P.M.C. found	Largest P.M.C. found	Mean	No. of cells
Meiosis	2100 units	15 045 units	6 695 ± 483	50
Mitosis	7202 units	21 207 units	12 014 ± 696	45
			t = 6,279	

The values obtained for the nuclei give a better view of the actual conditions. This is so because the P.M.C's themselves are dependent on the space available in the loculi and grow very unevenly on account of the different competition for space they have to meet (cf. BERGMAN, 1935 a, p. 226).

Figs. 129—138. *C. purpurea*. P.M.C's. — 129—135, mitotic division. 129, resting stage and prophase. 130—131, late prophase. 132, metaphase. 133, part of a loculus, only a few P.M.C's drawn. 134, plasmodium with two nuclei in division. 135, plasmodium with nuclei of different size in division. 136—138, type of division between meiosis and mitosis. All chromosomes not drawn. — Magnif. 1050 ×; 129, 133, 134, 138 = 540 ×; 135 = 360 ×.



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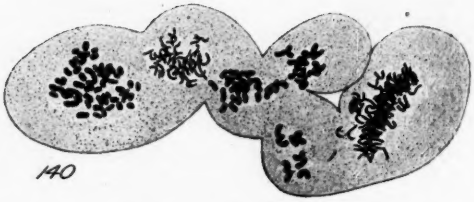

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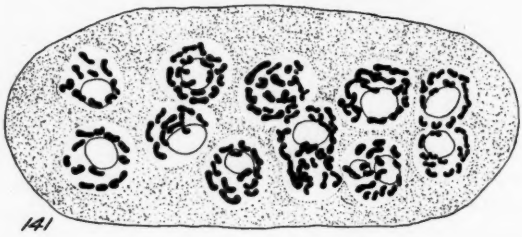

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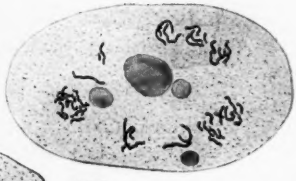

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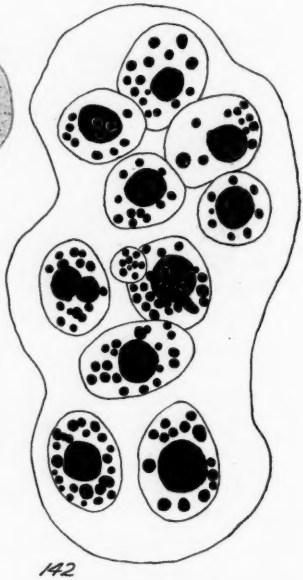

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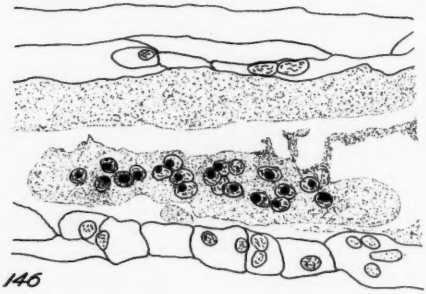

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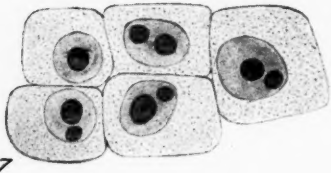

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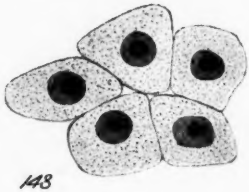

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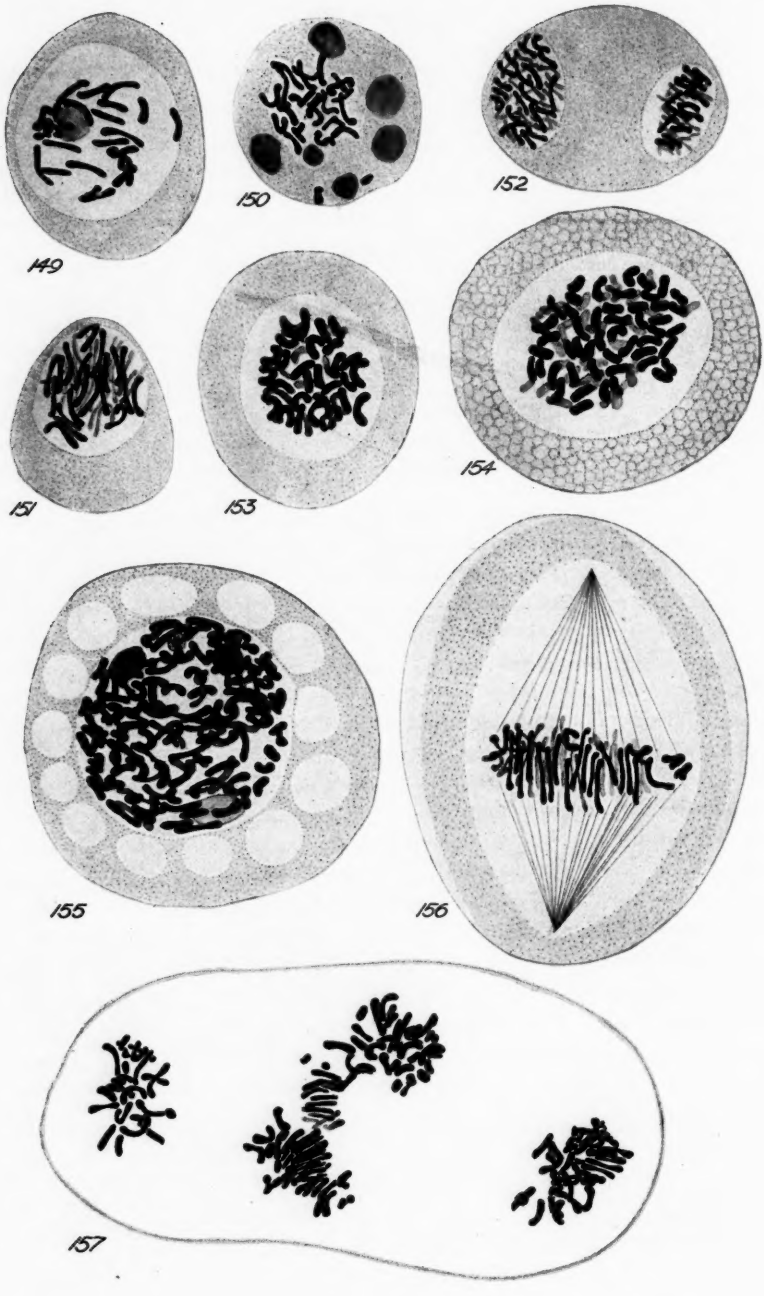
Method of measurement. — The volume of the nuclei and P.M.C's has been calculated by means of the formula $abc \cdot \frac{4}{3}\pi$ for the ellipsoid. The longest and shortest diameters of the nucleus have been measured, it being assumed for purposes of calculation that in one plane the nucleus is circular in section and in another elliptical. If the variation range for the length and breadth of the type is known, a nomogram can be drawn by means of which values proportional to the actual volume can be obtained direct. From a base-line two lines are drawn perpendicular to the base and at a certain distance from each other. On one vertical line log a^2 (in logarithmic scale, of course) is set off, on the other log b or log $b \cdot \frac{4}{3}\pi$. Centrally between the two perpendicular lines a third line is now drawn, also perpendicularly to the base, this third line being graduated in logarithmic scale with suitable units. When the volume is sought of a measured nucleus, a straight-edge is laid between the values for a^2 and b on the logarithmic scales. The volume or a quantity proportional to it is then obtained at the point of intersection with the third line. An appropriate graduation makes the measurement quick and simple.

As is evident from the synoptical scheme, two kinds of plasmodia occur, viz. with and without nuclear division. Plasmodia formed as a result of pre-meiotic fusions between cells that have retained divisions of meiotic or mitotic appearance only occur in the plant from Gällivare. In all the other plants sometimes a few P.M.C's, sometimes whole loculi coalesce and form plasmodia. If only a small number of cells are included, the plasmodium is rounded off in the loculus. At times only small plasmodia of this kind are present. These then lie at some distance from one another in the otherwise empty loculus.

If all the P.M.C's are united into a single large plasmodium (Fig. 146), no divisions take place. In the smaller plasmodia, on the other hand, the nuclei may sometimes start a division that is not completed (Fig. 141). In such cases the chromosomes are often scattered in the large cell. The number of nucleoli in the nuclei is very variable. As a rule, one or two large ones occur, sometimes a large number of small ones together with a large one. As in *C. lapponica*, P.M.C's often occur which never undergo division but remain in the resting stage until they degenerate. Such resting cells were found in all the examined plants. On degeneration the loculi collapse. Later on they dry up. The anthers are yellow in colour and do not dehisce. In the plant from

Figs. 139—148. *C. purpurea.* P.M.C's. — 139, plasmodium, formed by fused P.M.C's. 140, plasmodium with nuclei in mitotic division, contraction different. 141, plasmodium with started divisions. 142, plasmodium with many nuclei. 143—144, degeneration of the P.M.C's begins. 145, two P.M.C's, united to a »dyad». 146, plasmodium formed by a whole loculus. 147, resting nuclei of the mitotic type. 148, the same of the meiotic type. — Magnif. 600 ×; 140 = 350 ×; 146 = 240 ×.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Gällivare, however, they are purple and dehisce, at any rate in the first panicles.

If meiosis was strikingly polymorphous in *C. lapponica*, its uniformity is not less impressive in *C. purpurea*. Among 174 examined plants real divisions occurred to a more or less normal extent only in a single one. As will be seen later on (p. 171), however, the E.M.C's exhibit a more dissimilar behaviour.

Calamagrostis chalybaea.

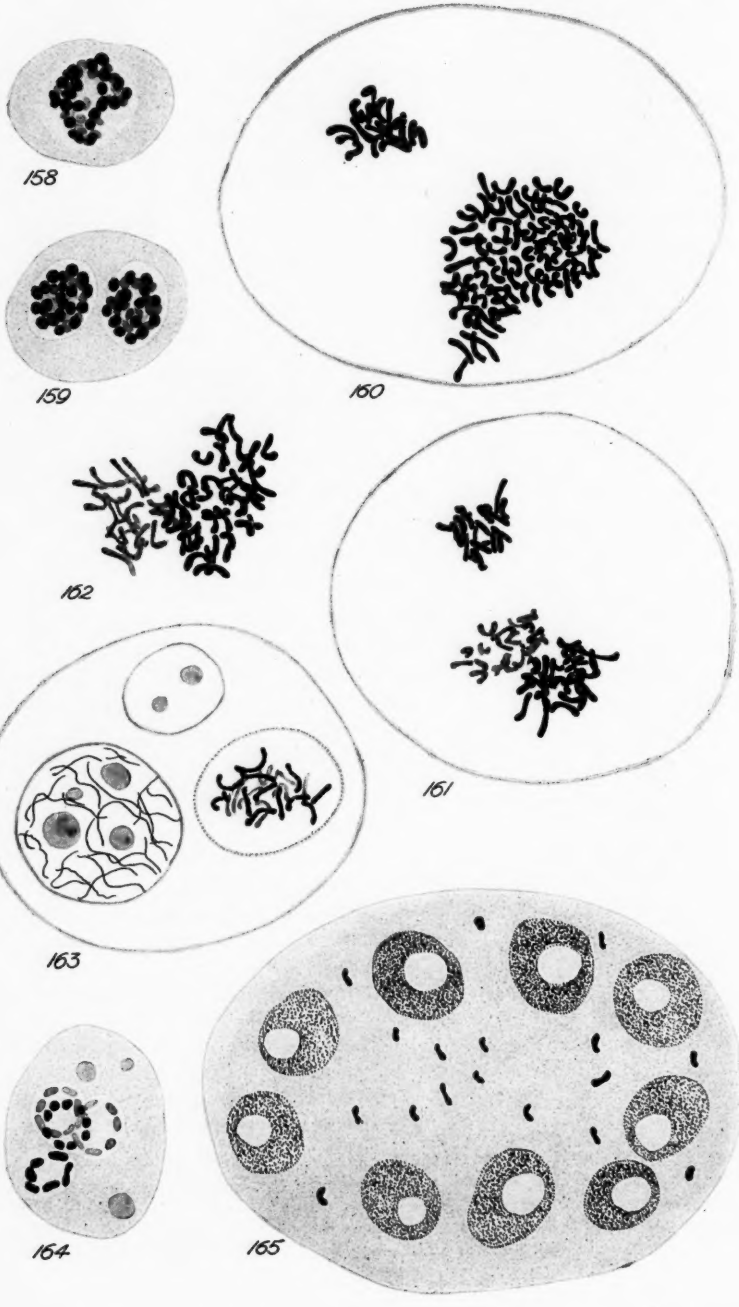
Chromosome number: $2n = 42$. Material: All the 11 plants included in the test were examined in sectioned material. The fixations were made in nature. One number with these first generations, 1—4, was fixed in the experimental field at Svalöf.

Pollen is not formed in *C. chalybaea*. In pollen preparations from crushed anthers pollen-like cells can be observed in great numbers. In this case it is a question of P.M.C's that have never undergone division but have been rounded off and detached themselves from other cells in the loculus. They thus occupy the same position as the resting cells in *C. lapponica* and *purpurea*. These old P.M.C's are very easy to recognize from the large number of small, rounded bodies that lie strewn in the plasm. Presumably these are drops of nutriment; similar drops have been observed in *C. purpurea*. The number of nucleoli is also remarkably high. This species is much less complicated than the previously described apomictic species.

Scheme showing behaviour of P.M.C's in Calamagrostis chalybaea.

I.	*Divisions occur.*	
	A. P.M.C's free.	1. Mitotic division.
		2. Formation of restitution nucleus in consequence of mitotic type of division. Extremely varying.
		3. Pre-meiotic fusions of P.M.C's give cells with the chromosome number $4n$.
	B. Plasmodium formation.	Direct consequence of above-mentioned divisions.
II.	*No divisions.*	Resting cells. Possess plasm filled with nutriment and nuclei rich in nucleoli.

Figs. 149—157. *C. chalybaea.* P.M.C's. Mitotic division. — 149, prophase. 150 and 151, late prophase. 152, anaphase. 153, metaphase. 154, metaphase in a cell with 84 chromosomes. 155, cell with 126 chromosomes ($= 6n$). 156, P.M.C. with the chromosomes in metaphase, the chromosome number is high. 157, plasmodium, different chromosome numbers in the groups. — Magnif. 1050 ×.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The mitotic type of division in the species examined reaches perfection in *C. chalybaea*. That the division will be mitotic can be seen even at an early stage in the P.M.C's. It is however delayed as in *C. purpurea*, and the P.M.C's often lie free from one another when division starts.

The 42 chromosomes form distinct equatorial plates, and the division proceeds as in normal mitosis (Figs. 149—156). As in *C. purpurea*, the contraction of the chromosomes varies much, but no resemblance whatever to meiotic univalents can be traced. The divisions are however difficult to find, the whole process presumably taking place at a rapid rate. In some cases differential staining with crystal violet-fuchsine-methyl green facilitated the work of finding divisions.

After the nucleus has divided once the cell may become binucleate until the next division occurs. However, restitution nuclei may also be formed. They may arise at very different points during a nuclear division and are formed in several different ways. In the P.M.C's the divisions continue irrespective of whether restitution nuclei are formed or not, with the result that at times the cells become gigantic. Perhaps this constitutes a form of polymitosis. The fact that the number of nuclei may be very variable is evident from the following table of 100 counted P.M.C's from different loculi:

Number of nuclei per P.M.C. in Calamagrostis chalybaea.

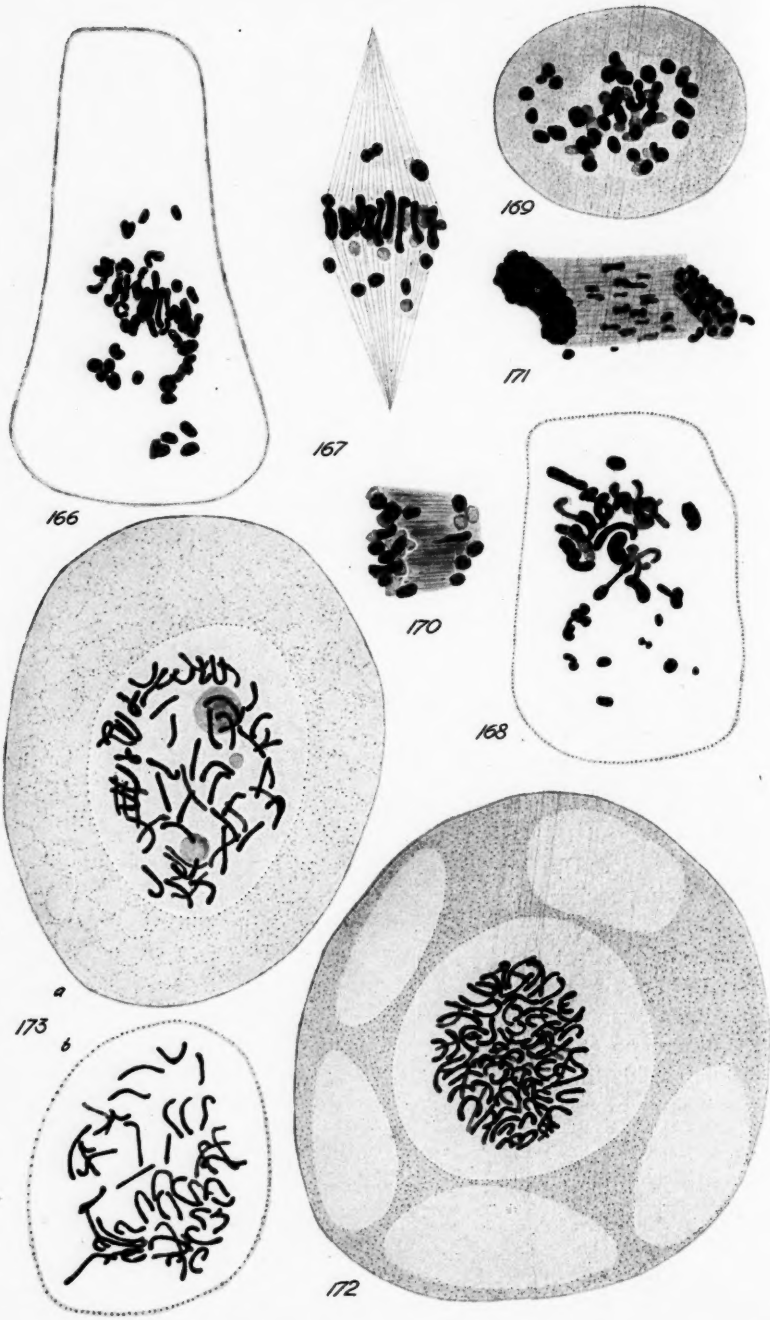
No. of nuclei..	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
No. of P.M.C's	48	7	3	6	12	5	4	3	1	1	0	2	2	1	0	1	1	0	1	1	1

It is immediately seen from the table that all nuclei do not divide simultaneously. On this account odd numbers often arise.

Certain peculiar disturbances have only been observed in *C. chalybaea*. Sometimes different numbers of chromosomes occur on the plates in spite of the fact that apparently no restitution nucleus is formed (Fig. 160). At times chromosomes are left out in the cell after a division. They then form micronuclei in the middle of the large cell (Fig. 165). Sometimes the chromosomes are divided into small groups that keep together inside the plasmodium (Fig. 164).

In some preparations a type of division with more contracted chro-

Figs. 158—165. *C. chalybaea*. P.M.C's. — 158—159, type of division with contracted chromosomes. 160, plasmodium with different numbers of chromosomes in the groups. 161—162, the same, in 162 only the chromosomes drawn. 163, plasmodium with nuclei of different size. 164, degeneration sets in. 165, plasmodium with many nuclei and with chromosomes spread in the cell. — Magnif. 1050 ×.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mosomes has been observed. It is rare and requires further study (Figs. 158—159).

In very early stages certain P.M.C's are found to be double as large as others. A pre-meiotic cell-fusion has thus taken place. The chromosome number in such P.M.C's will naturally be 84.

The profound disturbances which have transformed meiosis into a mitosis in *C. chalybaea* must be assumed to be genetically based. Nothing more definite can be said of this at the present moment. Similar cases are known from the genus *Hieracium*, these having been elucidated by ROSENBERG, GUSTAFSSON and GENTCHEFF. No case so pronounced as in *C. chalybaea* is previously known.

c. Embryo-sac mother cells.

Calamagrostis lapponica.

In this species two different types of division occur:

(1) Meiosis in disturbed form.

(2) Mitosis (STEBBINS, 1932; GUSTAFSSON, 1935, 1939; BERGMAN, 1935 a and c, 1941).

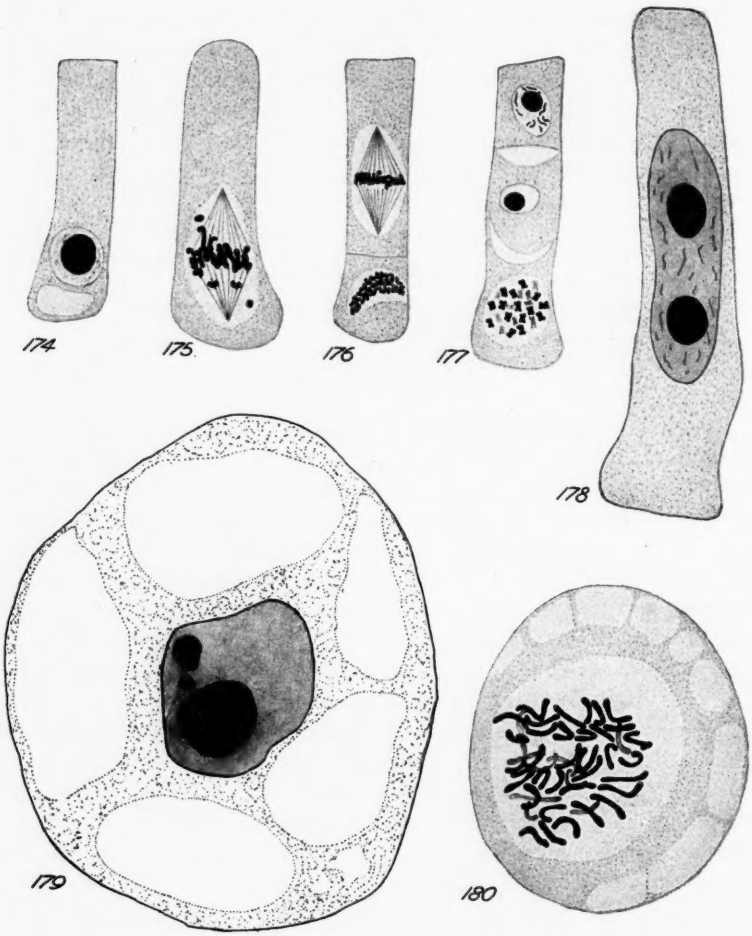
Three of the examined 28 plants possessed meiosis (Figs. 166—171). These plants belonged to the same population and had the chromosome numbers 105, 107 and 110. Only meiosis could be found in the 110-chromosomal plant, while the mitotic type predominated in the other two. In the first-mentioned plant first metaphase could follow the *Hieracium boreale* scheme. The univalents sometimes divide in first anaphase and telophase (Figs. 170—171). Unfortunately, older stages were missing of just this plant. In the other plants the development of the equatorial plates was disturbed at first metaphase by fragmentation (Fig. 168). Later stages than first anaphase were not discovered in spite of the very considerable material. Probably a degeneration of these E.M.C's therefore takes place at an early stage. In about 20.000 examined florets of *C. lapponica* 14 meiotic stages of division have hitherto been observed. This shows how rare such divisions are in this species. Certain morphological data suggest, however, that sexual gametes function at times on the female side.

The mitotic type of division is of the same kind as previously de-

Figs. 166—173. *C. lapponica.* E.M.C's. — 166, first metaphase ($2n = 110$). 167, first metaphase ($2n = 110$). 168, first metaphase ($2n = 110$), chromosome-fragmentation. 169, first metaphase p. v. ($2n = 110$). 170, first anaphase ($2n = 110$). 171, first telophase ($2n = 110$). 172, mitotic division, somewhat diagrammatical ($2n = 105 + 2$ fr.). 173, mitotic division with 98 chromosomes in a plant with $2n = 49$. — Magnif. 1100 ×.

scribed for several genera of plants, for grasses in *Poa* (KIELLANDER, 1935) among others. A survey of this type of division is given by GUSTAFSSON (1946).

Even at an early stage the purely mitotisized character of the chro-



Figs. 174—180. *C. purpurea.* E.M.C's. — 174—178, Gällivare 1—41. 174, resting nucleus. 175, first metaphase. 176, dyad. 177, triad. 178, restitution-nucleus? 179—180, embryo-sacs with one nucleus (*Antennaria* scheme). 180, mitotic division, all chromosomes not drawn. — All pictures from plants with $2n = 56$. — Magnif. 1100 ×; 174—177 = 550 ×.

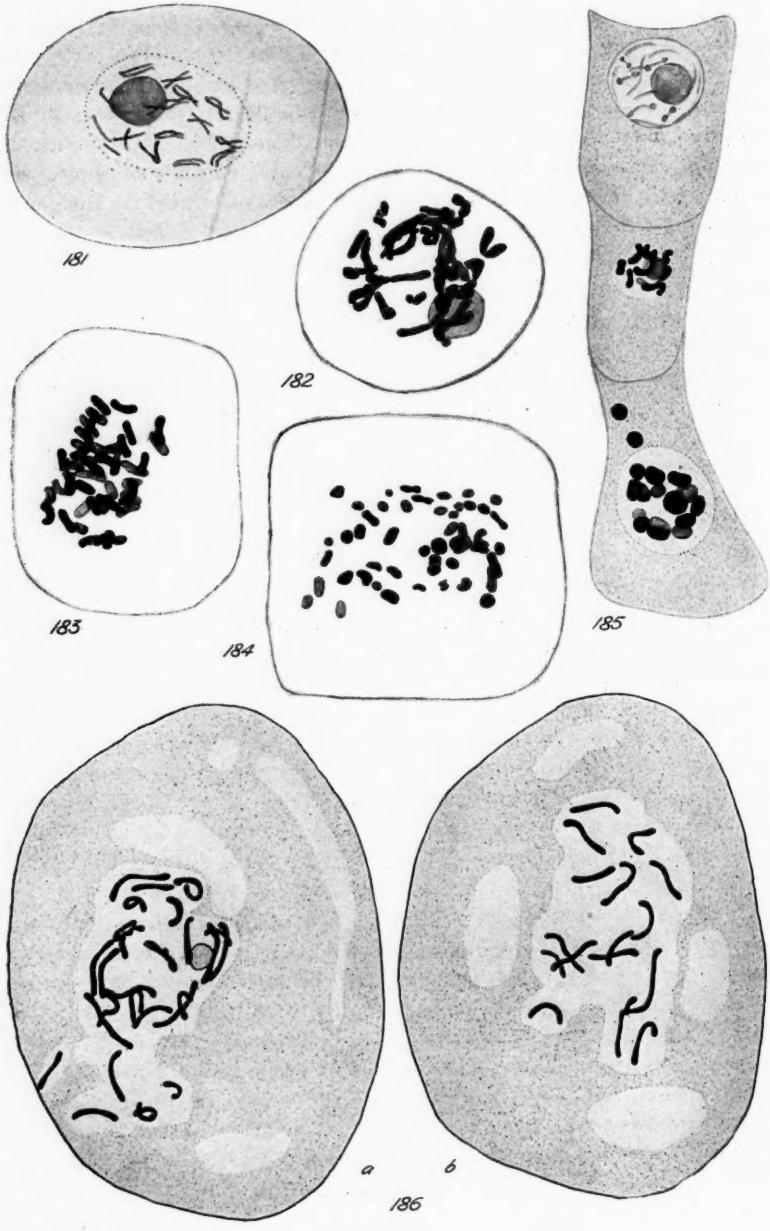
mosomes can be discerned; later they arrange themselves in the equatorial plane and undergo equational division (Fig. 172). Six such divisions were observed. In a plant from Porjus that showed great disturbances in the P.M.C's a doubling of the chromosome number occurred on the mitotic plate (Fig. 173). Presumably the doubling of the number from $2n = 49$ to $4n = 98$ was caused by a cold shock (see p. 155). This phenomenon has recently been demonstrated for the genus *Lilium* by ROSENBERG (1946). An interesting point is that in this cell with the doubled number not the slightest sign was discovered to show that pairing had taken place although at least 49 pairs must occur (GUSTAFSSON, 1934; cf. also STRAUB, 1939; M. CHRISTOFF, 1940). The mitotic type is apparently brought about by more profound causes than solely shortage of homologous partners when pairing starts.

Calamagrostis purpurea.

The same types of division occur as in *C. lapponica.* In *C. purpurea,* however, the female side deviates from the male side in so far that certain plants are able to undergo reduction division. On the male side this only occurs in a single plant among 174. Of the 119 plants examined in sectioned material meiosis occurred in the E.M.C's of 21, i. e. in 17,6 % of the plants. However, the occurrence of meiosis no doubt also depends in certain plants on external factors, and hence too great importance should not be attached to the above-mentioned figure (see further p. 183).

The meiosis was studied in the previously mentioned plant from Gällivare (p. 156). This plant, which on the male side had a greatly disturbed meiosis, exhibits regular meiosis in the E.M.C's. Only minor disturbances in the form of univalents and multivalents occur. Similar conditions are known in insect hybrids (FEDERLEY, 1931, p. 802). The botanical literature is cited in TISCHLER (1943, pp. 589—590).

The chromosomes are distinctly paired at pachytene. At first metaphase solitary univalents as a rule occur, these lying outside the plate. As a result the distribution of the chromosomes will be irregular. The chromosome number was determined in a triad (Fig. 177). The plate contained about 26 chromosomes, and therefore the nuclei should possess about 30. Later stages have not been found. Probably the triads degenerate, just as is known to occur in the genus *Poa* (KIELLANDER, 1941; HÅKANSSON, 1943). In one case an E.M.C. was found that seemed to contain a restitution nucleus (Fig. 178). However, no conclusions can be drawn from a single find.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The mitotic type of division was very difficult to find in *C. purpurea*, and so far it has only been possible to study one metaphase plate (Fig. 180). This presents no deviations from what was ascertained earlier in respect of *C. lapponica*. Before the nuclei divide both cell and nucleus grow much in size. The E.M.C. vacuolizes and the nucleoli of the nuclei become either strikingly large or notably many. If the number of nucleoli is large, they gradually fuse into one or more of considerable size.

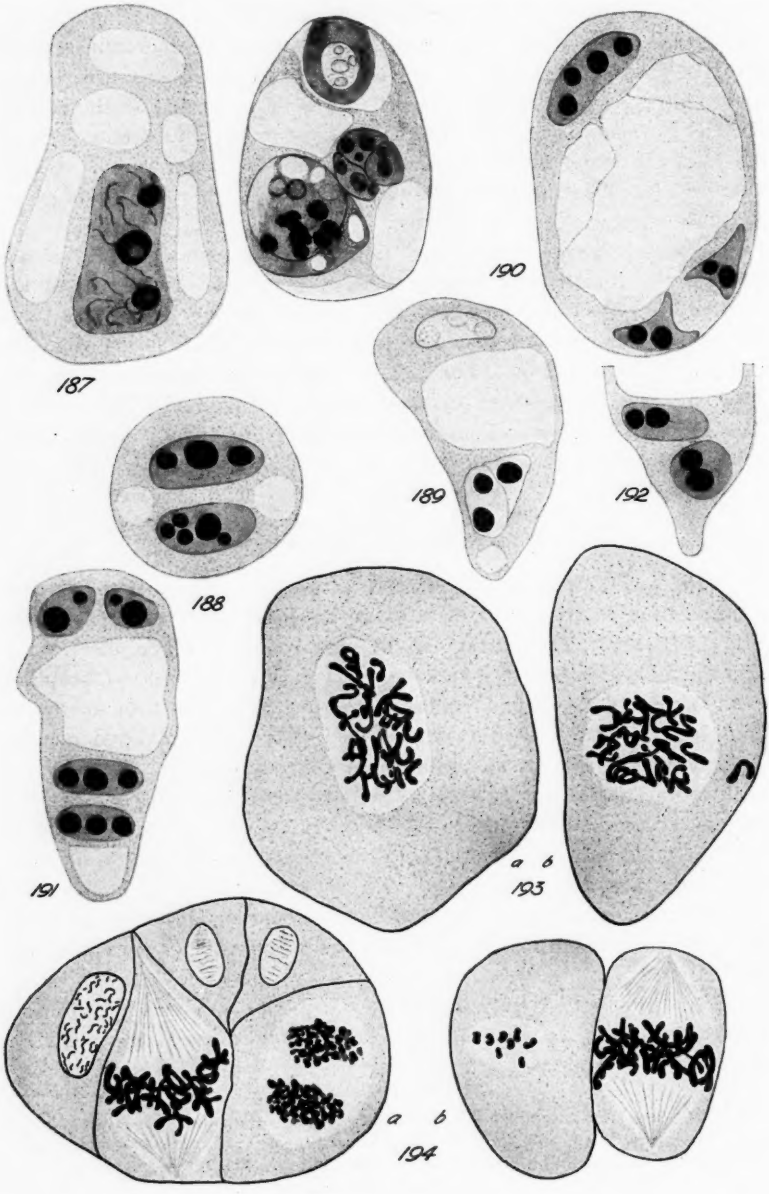
In some cases it has been possible to measure resting nuclei belonging to meiotic and mitotic types respectively. By means of the method described on page 163 the volume of the nuclei has been calculated. The mitotic nuclei were about eight times larger than the meiotic (cf. GUSTAFSSON, 1939, p. 295). However, this estimate is only approximate, as the shape of the mitotic resting nuclei makes exact measurement of their size impossible (Fig. 187). It was impossible to calculate the volume of the E.M.C's.

Calamagrostis chalybaea.

This species also behaves like *C. lapponica*. The meiotic division is interesting in that distinct pairing has been observed at diplotene (Figs. 181—182). Separation of the partners takes place later and at first metaphase exclusively univalents occur (Fig. 183). First anaphase exhibits chaotic conditions characterized by whole and split univalents (Fig. 184). Of the 11 plants examined only four possessed meiosis. Only one plate at first metaphase and first anaphase respectively has been found, and therefore other conditions than those mentioned above may be at hand. This species also behaves differently under dissimilar external conditions (see p. 183). In one case a triad of the *C. purpurea* type was formed (Fig. 185). To my mind this points to the possibility of more regular conditions occurring at first anaphase. Perhaps the division can proceed semiheterotypically or pseudohomeotypically.

The mitotic division has been studied at prophase (Fig. 186). A single division has been found in about 6.000 examined florets. The type has nothing new to offer.

Figs. 181—186. *C. chalybaea*. — E.M.C's. — 181, early and 182 late diplotene, paired chromosomes. 183, first metaphase, desynapsis. 184, first anaphase, chromosome-fragmentation. 185, a triad. 186, mitotic division in prophase. — Magnif. 1200 ×.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192
188
191
a b
193
a b
194

4. EMBRYOLOGY.

Amphimictic species. — Only general studies have hitherto been made of *C. canescens* and *neglecta*. Everything suggests that similar conditions exist here as in sexual *Poa alpina* (HÅKANSSON, 1943, 1944).

Apomictic species. — STENAR (1932) has studied the embryology of *C. chalybaea* (= *C. obtusata*) and *purpurea*. From the results of this study he has drawn the conclusion that at least *C. chalybaea* is reproduced by the parthenogenetic method.

Diplospory occurs in the species examined (EDMAN, 1931). The archespore is unicellular (STENAR, Fig. 1 *a*). The E.M.C. undergoes mitotic division (Figs. 172, 180, 186), and the egg-cell gives rise to an embryo (Figs. 193, 194) with or without fertilization.

After the first division the two nuclei pass each to its pole in the embryo-sac (Figs. 188, 189; STENAR, Fig. 1 *b*). The second division can proceed in the same way. Either the two nuclei divide transversally at the poles (Fig. 190), when, after completed division, they come to lie at each end of the sac. Or they divide in the longitudinal direction of the cell (Fig. 191). STENAR has observed a case in which a longitudinal division only takes place in that part of the embryo-sac which is normally occupied by the egg-apparatus (STENAR, Fig. 1 *c*).

The fully formed embryo-sac is of normal appearance as a rule. Occasionally, however, the division of the nuclei may vary.

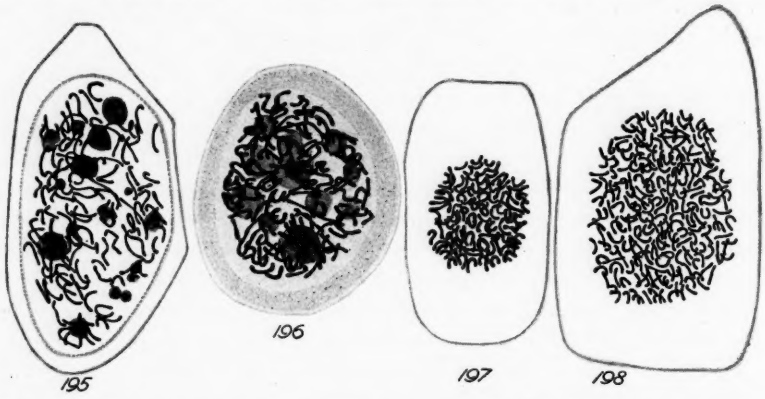
The polar nuclei vary in the present material between two and four. Four nuclei were found 7 times and three 6 times. Anomalies of a similar kind are already known from MURBECK's classical paper on *Alchemilla* (1902, p. 6).

During the further development of the embryo-sac a fusion takes place of the polar nuclei into a central nucleus (STENAR, Fig. 1 *h*), which in the majority of cases has the chromosome number $4n$ (Figs. 195, 197). (Cf. MURBECK, 1901, p. 31.) In some cases, however, the endosperm nuclei probably have the $2n$ number. This applies to *C. lapponica* and *purpurea* (Fig. 196). In these cases an exact chromosome count was impossible, however. Still, judging from their size, the endosperm nuclei in these species might very well have both the $2n$ and the $4n$ number (cf. JUEL, 1900, p. 47; STEBBINS and JENKINS, 1939, p. 213;

Figs. 187—194. *C. purpurea.* Embryology. — 187, to the left an uninucleate embryo-sac, *Antennaria* scheme; to the right an embryo-sac with egg-cell, 3 polar nuclei and 2 antipodes, the lower of which with many nuclei in division (240 ×). 188—189, first division. 190, second division longitudinally. 191, the same and transversely. 192, an »oblique» division. 193, egg-cell with 56 chromosomes. 194, embryo. All pictures from plants with $2n = 56$. — Magnif. 550 ×; 193—194 = 1050 ×.

M. A. CHRISTOFF, 1942, p. 175). In a case here and there two nuclei unite at a later division in the endosperm and plates with the 8*n* chromosome number are formed (Fig. 198), which are surrounded by tetraploid endosperm.

The divisions in the 8-nucleate sac always start in the polar nuclei or in the central nucleus. (The antipodal apparatus is not taken into account.) According to Fig. 2 *b* in STENAR the number of free endosperm nuclei in *C. chalybaea* may be considerable. The egg-cell, which at the outset is perfectly like the synergids, is at rest for a long time before it begins division. This does not take place until a large number



Figs. 195—198. Endosperm-cells. — 195, *C. lapponica* ($2n = 112$), about 112 chromosomes, but only half the cell is included, thus probably $4n$. 196, *C. lapponica* ($2n = 112$), endosperm diploid. 197, *C. purpurea* ($2n = 56$), endosperm $4n$ ($= 112$ chromosomes). 198, *C. purpurea* ($2n = 56$), endosperm $8n$ ($= 224$ chromosomes). — Magnif. 650 ×.

of nuclear divisions have occurred in the endosperm (cf. SCHNARF, 1929, p. 322).

The late development of the egg-cell that was determined with certainty in the present material for *C. lapponica* and *purpurea* and in STENAR's for *C. chalybaea* explains why hybrids can be formed between, for instance, *C. purpurea* and the amphimictic species. The chromosome numbers of these hybrids also clearly show that the number possessed by the functioning egg-cell must have been diploid (cf. ÅKERBERG, 1939, p. 366).

In one case, however, a hybrid plant was obtained that may have arisen through a sexual embryo-sac having functioned, but this plant died and could not be analysed ($2n = 48$).

C. chalybaea develops no hybrids so far as is known, while to all appearances *C. lapponica* hybridizes with *C. neglecta.* The high chromosome numbers of *C. lapponica* render it difficult, however, to investigate the chromosome numbers of the progeny.

Certain *C. purpurea* clones have given rise to twins. Presumably polyembryony occurs in this species. In the cases examined both twins have the same chromosome number (5 pairs from 2 clones). Twins are rather common in *Poa* according to ÅKERBERG (1942) and KIELLANDER (1942).

5. DISCUSSION OF CYTOLOGICAL RESULTS IN THE APOMICTIC CALAMAGROSTIS SPECIES.

The three apomictic species *C. lapponica, C. chalybaea* and *C. purpurea* possess certain cytological features in common while at the same time exhibiting considerable differences. A comparison of their cytological properties is summarized below.

Meiosis, apomeiosis and mitosis in apomictic Calamagrostis.

Species	P.M.C's		E.M.C's	
	Meiosis	Mitosis	Meiosis	Mitosis
C. lapponica	Regular—very irregular. Restitution nuclei common.	Occurrence not determined with certainty.	Regular—disturbed.	*Antennaria* type.
C. purpurea	*Hieracium boreale* and *laevigatum* scheme. Transmission meiosis—mitosis.	Occurrence determined in older flowers.	Regular. Restitution nuclei?	*Antennaria* type.
C. chalybaea	Absent.	Ascertained to be retarded.	Pairing at prophase. Desynapsis.	*Antennaria* type.

The scheme may be supplemented with the following facts:

(1) Regular reduction division in *C. lapponica* was not correlated in the P.M.C's and the E.M.C's (cf. GUSTAFSSON, 1938, p. 611). One plant with regular meiosis in P.M.C's showed exclusively mitosis in the E.M.C's. Another having a regular meiosis on the female side had a disturbed one on the male side.

(2) In *C. purpurea* the same plant presented the *Hieracium boreale*

and the *H. laevigatum* scheme in the P.M.C's and regular meiosis in the E.M.C's.

(3) In *C. chalybaea* the irregular division in the E.M.C's corresponds to a total failure of meiosis in the P.M.C's.

Similar conditions to those mentioned above are usual in hybrids according to TISCHLER (1943, p. 589). In certain genera such anomalies may depend on gene effects. For the genus *Datura*, for instance, BLAKESLEE and co-workers have devoted several investigations (1926—1936) to a study of the effect of recessive genes on the course of the reduction division. BERGNER, CARTLEDGE and BLAKESLEE (1934) have discovered a gene that to 92—98 % disturbs the development in the P.M.C's. In the same material BLAKESLEE, AVERY, BERGNER, SATINA, CARTLEDGE and BUCHHOLZ (1935 p. 39) found another gene that induced partial or complete failure of cell division and compound pollen-grains. This finding is in accord with the development of plasmodia in *C. lapponica* and *purpurea*, which as a rule is caused by an inhibition of the divisions and a degeneration of the P.M.C. walls in the whole or parts of the loculus.

That the breaking down of meiosis in certain apomicts is due to genic action has been accepted as a fact for a long time. Various investigators have trenchantly stated, however, that several processes interact here, and that these must be kept strictly separate. That agamospermy (TÄCKHOLM, 1923, p. 276) does not constitute a simple phenomenon is evident from such circumstances as the different degrees of syndesis found at the reduction division in P.M.C's and E.M.C's, the varying relation between meiosis and mitosis in P.M.C's and E.M.C's, and the fact that the property of forming unreduced embryo-sacs is present in some genera or species but absent in others. Agamospermy is therefore interpreted as a complex phenomenon that has probably arisen in different ways and by different processes within different genera. In the genus *Calamagrostis* agamospermy manifests itself in the species examined in the form of a diplosporous development of the E.M.C. and a breaking down of the meiosis in the P.M.C's. Similar conditions occur more or less pronouncedly in the other seven genera in which diplospory with mitotic division occurs, viz. *Antennaria*, *Arnica*, *Erigeron*, *Eupatorium*, *Eu-Hieracium*, *Poa*, and *Potentilla* (GUSTAFSSON, 1946). The central problem is here the relation between meiosis and mitosis. Important facts bearing on this relation have been submitted by ROSENBERG, BERGMAN, FAGERLIND, GENTCHEFF, GUSTAFSSON, STEBBINS, and others.

Since the omitted bivalent formation has proved to be due to a dissolved zygotene pairing (TAHARA, 1921, p. 31; LEVAN, 1940) caused by specific genes (BEADLE, MCCLINTOCK and associates), the reason for the occurrence of sometimes meiosis, sometimes mitosis in the P.M.C's and E.M.C's has come into the foreground (GUSTAFSSON, 1942 a). So early as in ROSENBERG's classical work on *Hieracium* (1917, p. 191) a type of division with mitotic chromosomes was described in the P.M.C's of *H. pseudoillyricum*. In 1935 (p. 53) GUSTAFSSON re-discovered this division in *Hieracium lapponicum* and BERGMAN in *H. umbellatum* (1935 b, p. 51), and in 1937 (p. 179) GENTCHEFF demonstrated the same type in *H. echioides*. It had then already been fully proved by STEBBINS's investigations of *Antennaria* (1932) that a mitotic type of division takes place in the E.M.C's of certain apomictic species of this genus. This had been observed earlier by HOLMGREN (1919, p. 87) in *Eupatorium glandulosum* without his being able to draw the full consequences of his find. STEBBINS's observations were subsequently confirmed in several genera (BERGMAN, 1935 a and c; GUSTAFSSON, 1935; KIELLANDER, 1935).

In his work on *Leontodon hispidus* BERGMAN showed (1935 a) that there was a mitotic division in retarded P.M.C's of this species. Referring to this condition he says (p. 229): »Wie sich aus dem Gesagten ergiebt, hat die abnorm verspätete Meiosis bei dieser Pflanze ihre Natur ganz und gar verändert. Die Paarung ist aufgehoben, und die Chromosomen haben in der Regel mitotischen Aussehen bekommen. Mit anderen Worten: die Teilung ist eine reine Mitose geworden, die in diploiden Tochterkernen resultiert.» This retarded division corresponds exactly with the conditions prevalent in *Calamagrostis chalybaea* and *purpurea*. As a rule those P.M.C's which do not undergo meiosis degenerate in these species. The mitotic division takes place only in solitary cells or solitary loculi. Similar observations have been made by FAGERLIND in *Wikstroemia* (1940, p. 32). The mitotic division appearing here was not retarded, however.

Mitotic divisions in the P.M.C's are best known from the genus *Hieracium* (GUSTAFSSON, 1935, 1939, 1942 a; GENTCHEFF, 1937, 1941; GENTCHEFF and GUSTAFSSON, 1940; GUSTAFSSON and NYGREN, 1946). Within this genus the mitotic division is always earlier than the meiotic; it has not been observed in retarded P.M.C's. GENTCHEFF and GUSTAFSSON consider (1940) that the earliness with which the division sets in is the cause of the alternate appearance in the same plant of bivalents, univalents and mitotisized chromosomes. In this connexion

special attention ought to be given to the division types which have an appearance intermediate between meiosis and mitosis. Intermediate forms of this nature are known from *Hieracium* (GENTCHEFF, 1937, p. 180, 1941, p. 145; GUSTAFSSON, 1942 a, p. 385) and *Wikstroemia* (FAGERLIND, 1940, p. 31). They also occur in *Calamagrostis purpurea*.

STRAUB (1939) succeeded in experimentally showing that in *Gasteria trigona* meiosis is converted into mitosis under the influence of high and, more especially, low temperatures. (Many authors have treated the problem of the influence of the temperature. A collection of the botanical literature is to be found in TISCHLER, 1943, p. 524.) Judging from STRAUB's experiments, the difference between meiosis and mitosis is chiefly dependent on the length of the prophase (1939, p. 453). It was long in meiosis and very short in mitosis. This rendered pairing impossible during mitosis.

From the facts given above the conclusion may be drawn that both external and internal factors can convert a meiosis into a mitosis. In several genera meiosis, mitosis and transitional forms between them occur even in the same floret. Over and beyond these there occur degeneration phenomena, formation of plasmodia and similar disturbances together with production of normal pollen. These conditions are not associated with any solitary family or families of plants, but occur in higher plants within several orders. There cannot therefore be any question of a monophyletic inheritance of these phenomena, and they must have arisen independently of one another in several families within the vegetable kingdom.

At an early point FUJII advanced the view that certain hormones influenced the development of the meiosis (ISHIKAWA, 1911). FAGERLIND (1937, 1944 a), GUSTAFSSON (1939, 1946), STEBBINS (1941), and others have taken up the same idea in recent years. These hormones have been normally transferred to the P.M.C's through the tapetal tissue (STEBBINS, 1941, p. 521), and therefore disturbances in this tissue can also be conceived as causing disturbances in the P.M.C's. Some support for this view is also to be found in the meiotic tendency occasionally exhibited by the tapetal tissue (FAGERLIND, 1944 a, p. 102, and lit. cit.). The way in which the hormones produced at meiosis can be conceived as acting is perhaps expressed most clearly by FAGERLIND (1944 a, p. 101): »In Anbetracht der Tatsache, dass die Makroarchesporzellen gewisser Agamogonen nicht die geringste Tendenz zu meiotischer Natur zeigen, und dass mehrere Agamogonen wechselnde meiotische Verhältnisse aufweisen, die den deutlichen Eindruck einer ganzen Übergangs-

reihe von reiner Mitose zu heterotypischer Teilung machen, liegt es meiner Ansicht nahe, anzunehmen, dass die Verhältnisse durch Mangel oder unzureichenden Bestand an Meiosis hervorrufenden Substanzen in den »Spormutterzellen» bedingt sind. Man kann annehmen, dass die Menge des Meiosis hervorrufenden Hormons einen gewissen Wert erreichen muss, damit die Meiosis normal ausfallen soll . . . . Sinkt die Menge des Hormons unter einen gewissen Schwellenwert, so ist das Resultat pseudohomotypische Teilung. Sinkt sie unter einen noch niedrigeren Schwellenwert, so bleibt die meiotische Natur ganz aus.» The conditions found in *Calamagrostis purpurea* obtain a very reasonable explanation if they are interpreted in accordance with FAGERLIND's above-mentioned view.

GENTCHEFF (1941, p. 148) attaches great importance to the time the division starts. The mitotic type of division is thought to arise when division takes place before the hormones produced at meiosis have had time to be formed. In support of this theory he adduces the relation between the divisions in the P.M.C. and the development of the tapetal tissue in *Hieracium umbellatum* f. *apomicta*. In my opinion it is of prime importance to decide *whether or not* such hormones are produced at all. When or how the distribution of the substances formed takes place is of secondary importance. It is probable, moreover, that plants behave differently in this respect.

Different parts of the same panicle in *Calamagrostis purpurea* could give different percentages of P.M.C's belonging to the *Hieracium boreale* and the *H. laevigatum* scheme respectively. This circumstance caused the present author to suspect that differences might also occur between panicles of different age. Examination of *C. purpurea* from Gällivare had shown that this plant possessed a semiheterotypic division in the P.M.C's and a regular meiosis in the E.M.C's. This was found in the material fixed in 1943, which consisted of a panicle from each of two clonal plants. The panicles were fixed at about the same time, which excluded later stages in the development of the E.M.C. These are not, however, necessary for an elucidation of the nature of the division, the difference between the meiotic and mitotic division being already ascertainable at an early stage.

In the summer of 1944 a number of fixations were made with a view to obtaining material of the later phase of meiosis in the E.M.C's. To ensure all stages being actually included the panicles were furnished with labels to show their age (all panicles do not, of course, shoot at the same time). Thanks to this measure it was possible to fix a large

number of panicles of different ages on the same day. At the general examination of this material the mitotic type of division was found to be common in the E.M.C's and to occur in the P.M.C's. A closer examination of the fixed material has yielded the data tabulated below. The fixations are taken in the order of the ages of the panicles. Large panicles were divided at the fixation. One panicle can contain over 500 florets.

Table showing occurrence of meiotic and mitotic types of division at different times during the period of vegetation in P.M.C's and E.M.C's of Calamagrostis purpurea.

Fix. date	Fix. No.	P.M.C's Meiosis	P.M.C's Mitosis	E.M.C's Meiosis	E.M.C's Mitosis	No. of fl.	With p.	E.M.C's	P.M.C's
8./6—43	135, 163	100 %	0 %	100 %	0 %	506	100 %	27	6.666
22/6—44	269, 270	30,8 %	69,2 %	45,5 %	54,5 %	344	46,0 %	66	2.672
22/6—44	244	8,2 %	91,8 %	71,4 %	28,6 %	134	1,5 %	7	122
22/6—44	271, 272	7,1 %	92,9 %	33,3 %	66,7 %	67	18,0 %	12	1.191
22/6—44	273, 274	0 %	100 %	29,4 %	70,6 %	109	1,8 %	17	359
22/6—44	279	0 %	100 %	27,5 %	72,5 %	402	0,5 %	80	5.042
						1.562		209	16.052

»fl.» = florets, »With p.» = Number of florets with pollen.

In the later fixations 273—279, plasmodia from cell-fusion occurred in almost every floret. Such plasmodia were entirely absent in fixations 135 and 163, i. e. when each plant developed only one panicle. When P.M.C. divisions at all occur in these later fixations, they are invariably mitotic.

The interesting point is not merely the altered meiosis—mitosis relation in various old flowers. More noteworthy is the behaviour of the plants during the first year, when only one panicle per plant is developed. The divisions in P.M.C's as well as E.M.C's were then meiotic. This fact seems to me to afford very strong corroboration for the previously advanced view respecting the stimulation of meiosis by certain hormones. The plants do not produce panicles until the root-system is well developed, which as a rule takes two years. Whether one or more panicles are formed is highly dependent on external factors, above all else on the weather during the spring. If the plant produces only one panicle, the hormone formed during meiosis is concentrated in this, while it is not sufficient in amount if the panicles should increase in number. According to this view, the disturbances thus increase with the number of panicles developed.

In order to investigate to what extent this view is applicable to the genus *Calamagrostis* or the species *C. purpurea*, the material from the plants fixed in the summer of 1943 was scrutinized. Among these, those were examined that had been planted out in the field in 1941 and that had formed panicles for the first time in 1943. Certain plants possessed only mitosis, 8 had predominantly mitosis, but one plant, Vansbro 2—41, $2n = 91$, had up to 90 % meiosis in the E.M.C's (50 cells counted). Material from the same plant, 1944, when it had grown strong, showed that solely mitotic divisions occurred.

An examination of *C. chalybaea* had given the result that the clone from Östersund, which had been cultivated since 1938 but was not fixed until 1941, had no meiosis on either the male or female side. A control showed, however, that material from natural populations in certain cases contained a reduction division in the E.M.C's. An analysis of the I_2 generation from the Östersund plant disclosed that meiosis in the E.M.C. also occurred in this plant. About 500 florets of the original mother clone (3 plants) had been studied on three different occasions during earlier years. In these 1.500 florets or thereabouts no meiotic E.M.C's had been discovered, whereas even a cursory examination of a young I_3 plant revealed such. As clonal plants are concerned here, this difference is not due to segregation or recombination.

The three cases cited above must be interpreted in a similar manner, and the following conclusion seems justifiable:

Certain apomictic species, which generally develop embryo-sacs by the diplosporous method through mitotic division, may also show meiosis. Which type of division gains ascendancy in the plant depends on the number of panicles and florets, something that stands in connexion with the age of the plant as well as with the nature of the weather during the earlier part of the period of vegetation. The same plant can therefore show, depending on the phenotypic conditions, different meiosis—mitosis relations year for year. This lability in the behaviour of the P.M.C's may at times cause a complete suppression of the meiotic division. If the plant has any propensity at all for developing meiosis, this may occur certain years either in the same plant or in its progenies. This fact may also be expressed thus, that the genotype of the plant carries with it the possibility of the meiosis varying year from year, depending on the physiological conditions that exist.

About the same time as these facts became known, GUSTAFSSON obtained extremely important results from his experiments with *Hieracium robustum* (GUSTAFSSON and NYGREN, 1946). This South-

European *Hieracium* species was cultivated in experimental fields in the Botanical Garden of Lund, in hot as well as in cold houses. The plants grown in the field developed in 1942 a mitotic division in the P.M.C's, while those grown in the hothouses showed only meiosis. In this material a very distinct difference was observed in the development of different types of division in 1939 and 1942 (cf. pp. 5 and 6). In 1939, for instance, the mitotic type of division did not occur at all. This examination has thus yielded results analogous to those obtained for *Calamagrostis*.

From these investigations we now know that in certain biotypes within a species meiosis is liable to be transformed into mitosis under the influence of external condition, heat, cold, drought, etc., but also that the genotype of the plant may be of such a nature that one of the division types is normally suppressed and only developed under special external conditions. The dividing-line between meiosis and mitosis is at times so vague that the supply or lack of a specific substance results in sometimes one, sometimes the other type of division gaining the ascendancy. Whether these substances or hormones are developed or not is connected in certain cases with external factors.

Judging from these experiments, it cannot be definitely stated that a certain examined apomictic species showing the above-mentioned mode of reproduction (diplospory with mitotic division) has no meiosis. In the present writer's opinion, however, later investigations will probably show that, even in the same environment, different biotypes of a species possess different capabilities for developing the meiotic or the mitotic types of division.

The fact that other kinds of apomixis than agamospermy can also be influenced by external conditions is evident from an investigation by LAWRENCE (1945). LAWRENCE has cultivated *Deschampsia caespitosa* in California under different external conditions (see CLAUSEN, KECK and HIESEY, 1940). In his experiments, besides American types, some Swedish and one Finnish were also found. All had the same chromosome number ($2n = 26$, p. 302). On cultivation the Scandinavian forms became viviparous. »All of the European races became vegetatively apomictic (viviparous) in the transplant experiments, though only half of the individuals were strongly so. This phenomenon is not known to occur in the European habitats of this species, nor in the native Californian races» (p. 313). LAWRENCE considers that the morphologically similar ecotypes are physiologically dissimilar. They therefore behave diversely in different environments, since the physio-

logical differences manifest themselves independently of the morphological ones.

In this connexion reference should be made to the statement made on page 155 to the effect that *C. lapponica* plants fixed up in the alpine region did not develop meiosis but only gave fusion plasmodia. Such plants were also found in subalpine regions, though in them some type of division was always found. *C. neglecta*, growing in the same environment, presents solely a regular meiosis so far as the author has been able to ascertain (cf., e. g., FLOVIK, 1938, p. 282). Disturbances in an apomictic *Calamagrostis* species, therefore, need not by any means signify that an amphimictic species must also exhibit such, even under similar abnormal external conditions.

BABCOCK and STEBBINS (1938, p. 49) and STEBBINS (1941, p. 532) consider that the obligate apomicts have originated from the facultative, at least in the majority of cases. Within the same species there are often total apomicts without any meiotic tendency, such with varying meiotic tendency and facultative apomicts. It is thus evident that the line of demarcation between these three categories may be rather difficult to draw and that in different years the same plant may occur in all the three above-mentioned shapes. What applies to the individual plants will also naturally hold for their parthenogenetically produced progeny, as is indicated by the conditions in *Calamagrostis chalybaea*.

Tables of the kind set up by BERGMAN (1941, p. 17) of various species within the *Archieracium* complex can only be regarded as possessing applicability to the examined type under the conditions existing when the plants were fixed. Other types may give quite different values, the plants examined may give different results on examination another year when the number of heads, etc. is different. Another concrete example will be submitted in this question. In three different papers an *Erigeron* species [= *E.* cf. *annuus* = *E. ramosus* (WALT.) B. S. P.] cultivated in the Bergian Garden in Stockholm has been described (HOLMGREN, 1919; GUSTAFSSON, 1935; BERGMAN, 1944). The results differ rather much. This may naturally depend upon the examinations being carried out with different degrees of thoroughness, but also on the fact that the species, like, e. g., *Calamagrostis purpurea*, has developed differently in different years.

That the phenotype is a function of the genotype and the environment is a fact that has been long known by geneticists. This must also be borne prominently in mind at cytological investigations. The degree of variation shown by a material must be tested under different en-

vironmental conditions — it is not sufficient to draw general conclusions from examinations of one or two specimens of a species obtained from a botanical garden somewhere. Fixations made at the natural locality of the plant will no doubt give better results in this way than those made in experimental fields and laboratories, just as they will also give an indication of the range of variation. Even in the case of such fixations, however, attention must be constantly directed to the annual variation in rainfall, cold, warmth, etc. at the growing-place, since these factors influence the course of the reduction division.

III. ANALYTICAL STUDIES OF POPULATIONS.

1. AMPHIMICTIC SPECIES.

The amphimictic *Calamagrostis* species in Scandinavia are very easy to distinguish from one another. A couple of them, however, are liable to be confused with two of the apomictic species.

During the very first phase of the investigations it became clear that the amphimictic *Calamagrostis* species are cross-fertilizers (p. 133). This results in an effacement of the dividing-lines between different forms of the species. WESTERGAARD (1943) has already shown that habitat modifications are common in *C. epigeios*. This also applies to all the species treated in this work. Still, it has been successively found that real varieties are formed in certain species, whereas in others there are all possible transitions between extreme types. The cause of this has admitted of being explained through crossing experiments. The species dealt with are *C. epigeios* $2n = 56$, *C. neglecta* and *C. varia*.

A. CALAMAGROSTIS EPIGEIOS (L.) ROTH.

[Tent. Fl. germ. I (1788), p. 34.]

The species belongs to the commonest of Swedish plants. It is easy to recognize from the characters given in the floras. The species grows preferably in large, sparse, sometimes sterile groups in rather light soils. It is especially common along highways and railways. In its localities the species is extremely robust in growth. It develops stolons in great numbers, in a few years a single plant may spread over several square metres. The species is very resistant to cold and drought; after a heavy rainfall the number of stolons will increase. It has therefore become a troublesome weed that makes its way along newly constructed roads in search of areas where it was previously missing.

The *C. epigeios* growing in Scandinavia has the chromosome numbers 28 and 56. There are, to be sure, also plants with $2n = 42$, but these are rare. To distinguish between plants with the numbers

28 and 56 by their habit is difficult. WESTERGAARD (1943) states that although the two chromosome races can be separated when they occur in the same locality they do not possess satisfactory characteristics by which to distinguish them from each other in all situations.

In the summer of 1943 measurements were made on both the chromosome races of *C. epigeios* in order to determine whether they could be differentiated macroscopically. The measurements comprised length of straw, length and width of panicle, length, breadth and thickness of leaf, and the relation between the length and width of the panicles as well as the length and breadth of the leaves (cf. MÜNTZING, 1936). Twenty-three plants with the chromosome number 28 and twenty with the chromosome number 56 were measured. The measurements were carried out twice with a fortnight's interval. Ten measurements per plant were made each time, each final figure thus being the result of altogether 20 observations.

Table showing measurements on Calamagrostis epigeios.

2*n*	S-l cm.	P-l cm.	P-br cm.	L-l cm.	L-br cm.	L-th cm.	P-l/P-br	L-l/L-br
28	104 ± 2,5	19 ± 0,1	8 ± 0,4	30 ± 0,5	0,9 ± 0,01	2,2 ± 0,06	2,5 ± 0,2	32,9 ± 0,97
56	109 ± 2,9	21 ± 0,4	8 ± 0,2	31 ± 0,9	1,2 ± 0,03	2,8 ± 0,07	2,6 ± 0,07	25,0 ± 0,87

S-l = straw-length. P-l = panicle-length. P-br = panicle-breadth. L-l = leaf-length. L-br = leaf-breadth. L-th = leaf-thickness (10 times the thickness of the leaf has been measured).

It will be seen from the table that the leaves are broader in relation to the length and thicker in plants with the chromosome number 56. The measurements were made on the uppermost straw-leaf; the *t* values obtained are fully significant; $6{,}063^{***}$ for breadth/length, and $6{,}508^{***}$ for the thickness (BONNIER and TEDIN, 1940, pp. 44—45).

The same summer the length of the anthers was measured on twenty-seven tetraploid plants and twenty-two octoploid. In this case the measurements were made just before the anthers had dehisced on three different occasions at weekly intervals. Every value is thus based on 30 observations per plant.

Mean length of anthers in C. epigeios.

2*n*	Value
28	2,0 ± 0,05
56	2,5 ± 0,03

The ratio 56 : 28 gave a t value of $8{,}575^{***}$. It was also found that the width of the anthers gave higher values in the octoploids than in the tetraploids, and hence the volume of the anther is larger in the octoploid.

In his work of 1943 WESTERGAARD also states that as a rule the stomata are larger in plants with 56 chromosomes than in those with 28, though the same leaves may have stomata of different sizes (p. 10). This has been verified in the present examinations. The size of the pollen according to measurements by WESTERGAARD (l. c., p. 9) averages 34,04 units in the octoploids and 28,18 in the tetraploids (means worked out by the present writer). This has been confirmed here, approximately the same figures having been obtained. The values for morphologically good pollen given by WESTERGAARD (1943, p. 10) does not, however, agree with those now found (see p. 233).

With the aid of the above-mentioned leaf and anther characters it was possible to distinguish the tetraploid from the octoploid *C. epigeios* in the herbaria. Judging from the distribution of the two types, the octoploids are able to endure more extreme conditions. They are not only common along the Swedish coast but also occur in or in the immediate proximity of the mountains, where the tetraploids are entirely absent. This distribution is an interesting parallel to that of the species-complex to which *C. canescens* belongs.

The characters recorded are very easy to apply in nature for a study of the variation within the species. Both the chromosome races behave differently in this respect. Most of the »forms» of *C. epigeios* ($2n = 28$) are only habitat modifications. In only one case has it been possible to discover a distinctly deviating genetically controlled variety. It originates from Dalsland and differs from the common *C. epigeios* by its long, pendulous leaves and a panicle of different form and colour. In addition it is unusually low in growth.

The 56-chromosomal complex, on the other hand, forms distinct varieties. In nature one and the same octoploid variety of *C. epigeios* may be encountered within large areas. It is especially common along road-edges and railway banks in Norrland. If tetraploid and octoploid types occur together, the difference is very obvious. The tetraploids vary, but the variations merge into one another, while the octoploids are constant. This was originally interpreted by the writer as a consequence of intraspecific ploidy conditions. FLOVIK (1938) has shown that *C. neglecta* ($2n = 28$) possesses four identical chromosome sets and is therefore tetraploid. There is thus no reason to regard, as did

WESTERGAARD (1943), 28-chromosomal *C. epigeios* as diploid; it must be interpreted as tetraploid and the 56-chromosomal race as octoploid.

In crossing experiments between *C. epigeios* ($2n = 56$) on one hand and other European amphimictic species including *C. epigeios* ($2n = 28$ and 42) on the other it has been observed that octoploid *C. epigeios* is capable of self-fertilization after pollination with pollen from a foreign species or from tetraploid or hexaploid *C. epigeios*. Under these conditions it is thus self-fertile. WESTERGAARD reports (1943, p. 42) that crosses between 28- and 56-chromosomal *C. epigeios* in both directions gave 42-chromosomal progeny (triploid according to WESTERGAARD). With the octoploid as mother this cross was carried out twelve times (146 chromosome-counted F_1 plants), in addition to which in 37 crosses (259 F_1 plants chromosome-counted) pollen from all amphimictic *Calamagrostis* species in Europe has been applied without any hexaploid hybrid being produced in a single case. In all the cases the progeny was identical in type with the maternal parent and possessed the latter's chromosome number or a higher one. Crosses between octoploid and hexaploid *C. epigeios* with the octoploid as mother gave similar results. The same applies to crosses between octoploid hairless and hairy *C. epigeios*; the offspring have in all cases been of the maternal type. There is no doubt that certain biotypes within the octoploid race of *C. epigeios* occur in nature as self-fertilizers. For this reason the octoploid ought to be able to form pure lines.

The octoploid race of *C. epigeios* must be considered to have arisen from the tetraploid of the same species. The most important possibilities for their origin are as follows:

(1) By somatic bud mutation.

(2) By unreduced gametes.

(a) Direct or with twin formation.

(b) The developmental series 28—42—56.

(3) Doubling of chromosome number in the zygote.

(1) In root-tips of both tetraploid and octoploid *C. epigeios* chromosome plates with the double number have been observed on solitary occasions. Whether whole shoots with these numbers can be formed is an open question.

(2) That certain tetraploid *C. epigeios* plants have the power to produce macropollen has been established in pollen tests. These pollen grains are probably unreduced gones. It is probable that embryo-sacs with unreduced chromosome numbers in the egg-cell occur in *C. epigeios*. In one case tetraploid plants on being crossed gave rise to four F_1

plants possessing the chromosome number 42 (see p. 226). In another a dodecaploid plant was obtained after a cross between two octoploids. The chances of an octoploid being formed direct are small, however. On the other hand, hexaploids undoubtedly arise now and then from tetraploids.

Twin plants with double the chromosome number of the maternal plant are rare. However, one such plant arose in *C. arundinacea*, and therefore this possibility is also open in other species.

(3) Doubling of the chromosome number in the zygote is conceivable. In the case of *C. lapponica* it was possible to show that a doubling of the number took place in a uninucleate embryo-sac with mitotic division.

Hexaploid *C. epigeios* sometimes possesses the ability to form unreduced gametes. Presumably, different hexaploids can behave differently in this respect. From hexaploid *C. epigeios* descendants with both high and low chromosome numbers were obtained. The progeny with the high chromosome number seems to become stabilized around the number 56, while the offspring with a low number tend towards 28. Crossing experiments have shown that tetraploids and octoploids can be formed in this way. Besides these, only plants with the chromosome numbers 28, 42 and 56 have been found in natural populations. As a matter of fact, it is a well-known fact that aberrants behave in this way (for *Dactylis*, see MÜNTZING, 1937).

It is quite obvious that hexaploids can give rise by the above-mentioned method to an unlimited number of new types with the chromosome numbers 28 and 56. If one or more hexaploids arise in a population of tetraploid *C. epigeios*, there will probably emerge octoploids in the group after some time. Through mutual crosses new types with the chromosome numbers 28, 42 and 56 can be formed in the population.

If *C. epigeios* ($2n = 28$) and *C. arundinacea* grow together, they are liable to form hybrids. These hybrids back-cross in certain cases with the parent species and often it is impossible to distinguish definitely between the back-cross plants and the parents. As it is here a question of tetraploids there are, however, great possibilities that such back-cross plants (or F_2 progenies) possess within them genes from the other species which do not alwalys manifest themselves in the phenotype (for *Salix*, see HERIBERT NILSSON, 1918, 1930; for *Viola*, see CLAUSEN, 1926, p. 97; for *Malva*, see KRISTOFFERSON, 1926, p. 271; for *Galeopsis bifida* and *Tetrahit*, see MÜNTZING, 1930 a, p. 328).

If such a back-cross plant produces unreduced gametes, these may carry with them to a possibly formed hexaploid genes from another species in a single or higher set. Should such hexaploids give rise to octoploids, e. g. through self-fertilization, these genes from *C. arundinacea* may also be introduced into the octoploid. Such a condition has been observed by the writer in habitats where both the species occur together. In one case tetraploid and octoploid *C. epigeios* grew together with *C. arundinacea* along the edge of a road on Gräsö in Upland. All of them form a vast mixed complex. The ten octoploids from there that were cultivated show distinct traces of *C. arundinacea* in their more tussocked mode of growth, colour of the plants, venation of the leaf surface, etc. Especially the differences in colour are very striking.

Now and then *C. epigeios* plants are also met with that are perfectly sterile and only able to propagate vegetatively. A tetraploid plant of this kind from Boxholm in Östergötland regularly possesses a normal meiosis, a high percentage of morphologically good pollen, and good pollen-germination. It was however impossible to obtain progeny from the plant in spite of all conceivable crosses being attempted. There may be a variety of reasons for this. Similar experiences have been recorded from certain artificial hybrids. It is therefore not excluded that this plant is sterile as a consequence of former hybridization.

As previously mentioned, the octoploids possess the property of self-fertilization. There thus exists a tendency to homozygotization in this race. This may account for the relatively small disturbances in the meiosis, the good pollen fertility as well as the slight segregation in crosses between »sister-plants».

The variation within different forms of the chromosome race is wide. At times extreme plus and minus variants arise. One octoploid plant from Upland had a 3-centimetre wide leaf and a very robust growth, while another from Hälsingland was as bad as a minus-variant that has arisen in an F_1 of octoploid *C. epigeios*. The worst hybrid plants generally die rather soon, and therefore such individuals are presumably immediately eliminated in nature.

Crossing experiments combined with studies in nature show that the variation in *C. epigeios* is enormous but that to all appearances it is controlled by different conditions in tetraploids and octoploids. On the whole the tetraploids are true cross-fertilizers, even if they can now and then be stimulated by foreign pollen to self-fertilization. They therefore exhibit the variation typical of cross-fertilizing plants, which gives rise to transitional types between the different varieties arising.

True ecotypes have not been formed or are very rare in the Scandinavian region. The octoploids are chiefly reproduced by self-fertilization. They form varieties. Probably it is more than mere chance that the octoploids have principally taken possession of coastal and montane districts. Along newly constructed roads and railways in Norrland the octoploids conquer new ground for the species at the same time as the tetraploids disappear in many places. The hexaploids are the source of new tetraploids and octoploids, from which Nature herself creates new varieties through selection.

B. CALAMAGROSTIS NEGLECTA (EHRH.).
[Fl. d. Wett. I (1799), p. 94.]

This species may be confused with *C. lapponica*. It is most easily recognized by the callus hairs, which are shorter than the lemmas, as well as the hispid leaves, which are furnished with raised nerves. Furthermore, the florets are seldom more than 3—4 mm. long in this species, while they may be up to 8 mm. long in *C. lapponica*. In its natural localities *C. neglecta* usually grows in moister places than *C. lapponica*.

The very first isolation experiments showed that *C. neglecta* was not an obligate cross-fertilizer. This became still clearer from the results obtained in the crossing experiments. So far, with the technique used, only in one case has it been possible to produce hybrids with *C. neglecta* as mother.

The multiplicity of forms within the species cannot solely depend on habitat modifications. Certain montane forms are difficult to keep under cultivation. At least one and probably several lowland varieties occur. The lowland forms are usually tall, during anthesis they have pale-grayish outspread panicles and leaves, which may be more than one centimetre broad. This lowland-series, which is common in the more southerly parts of Norrland, also extends up into the mountains but usually does not reach beyond the tree-limit.

In the alpine region another form-series is predominant. Its forms are low in growth, have spike-like, compressed panicles and very pruinous, usually broad glumes. They can be encountered also in many places in the forest-land of Norrland. Taxonomically they agree with *C. neglecta* var. *borealis* LAEST. According to HULTÉN (1942, p. 168), this variety deserves the dignity of species.

There probably exist several ecotypes of the lowland as well as of the montane series. The progeny has been studied in a couple of cases.

Plants from Norrbotten gave progeny of the same type as the mother. The same was the case in a form from North Jämtland. Both belong to the montane series.

In nature *C. neglecta* behaves like octoploid *C. epigeios*. A certain form may dominate in large areas of the country, while other forms appear in similar localities in other places. Evidently several genotypically separated complexes occur. The occurrence of different forms within the same area in the same or similar localities has been specially studied by the author in northernmost Sweden.

For a stretch of 150—200 miles along the River Muonio one and the same *C. neglecta* type occurred. It was usually sterile on the river-banks. It looked exactly the same at Karesuando in northernmost Lapland as at Areavaara 150 miles to the south. — At Karesuando, however, another type dominated that occurred in masses on the river-banks between the church village and Kuttainen, about fifteen miles to the northeast. This type was tall, more rarely sterile, and could grow in drier localities than the first type. — By some lakes that are in communication with the River Muonio a third type occurred. It was creeping, slender, grew almost entirely under the surface of the ground and flowered extremely sparingly. It occurred in broad belts along the lakes, mile after mile without variation. — Along the road between Karesuando and Kuttainen, finally, there was a fourth type. This type was fairly tall and grew in thousands of individuals along a stretch of about three miles. The plants were perfectly constant. Thus, within this small area, a circle having a radius of 7—8 miles, there were four different types of *C. neglecta*, three of which in exactly the same environment. The three types first mentioned even grew all mixed up in a couple of places. All four types had the same chromosome number: $2n = 28$.

At Lake Åre in Jämtland the writer had an opportunity of studying a mixed population of *C. neglecta* and *C. epigeios*. A very rich material was collected here; all the plants had the chromosome number 28. It was interesting to observe that certain characters in some plants suggested a strain of *C. epigeios*. Generally this came out in the length of the callus hairs in relation to the lemma, in the shape of the glumes, degree of leaf hispidity, etc. Practically the whole population consisted of transitional forms to *C. neglecta*. The transitional forms, however, formed natural units inside the large population, and it was very easy to distinguish them in their locality. A few hundred metres from the population just mentioned was the type illustrated in Fig. 207, lower

row (p. 217). It does not look like an ordinary *C. neglecta* but in much resembles the apomictic species *C. lapponica*.

In their behaviour these natural populations show many similarities to the octoploid in *C. epigeios*. When the species goes over to self-fertilization, biotypes and, possibly, ecotypes are formed that are suited to a different environment. It is thanks to the exceptional capacity of the species to propagate vegetatively also, by stolons, that these types can obtain so wide a distribution as the specimens from the Karesuando district indicate.

C. neglecta has a remarkable power of adaptation. In the Swedish alps, at 67° northern latitude, it extends up to 1.300—1.400 metres above sea-level. In distribution *C. neglecta* is arctically circumpolar and occurs both in Greenland and Spitzbergen (HULTÉN, 1937, 1942; FLOVIK, 1938). In spite of this the species is found in Central Europe. Such an extensive range is not shown by any of the other European species, not even *C. epigeios*.

On account of the situation during the World War it has not been possible to investigate the chromosome number of Central-European *C. neglecta*. Maybe it has a higher chromosome number than its counterpart in the north. The climate of Central Europe may very well be critical for such an arctic-subarctic species.

C. CALAMAGROSTIS VARIA (SCHRAD.) HOST.
[Gram. Austr. IV (1809), p. 27.]

The species is tufted like *C. arundinacea*, both of which species belong to the group Ancylathera (TORGES, 1898), which is characterized by powerful awns, that are genuflexed after drying. In *C. varia* these awns seldom shoot above the glumes as in *C. arundinacea*, in addition the callus hairs in this species are almost as long as the lemmas, while in *C. arundinacea* they are very short.

In Scandinavia *C. varia* occurs only in Gotland. It is a peculiar species that is not connected with the rest of the Nordic flora, but rather constitutes a last outpost of the Central-European. Phytogeographical parallels to this species occur in Gotland as well as Öland.

All conceivable combinations between *C. varia* from Gotland and other European amphimictic species within the genus *Calamagrostis* have been made. It has been quite impossible to obtain any seed. The species neither produces hybrids nor is it stimulated to self-fertilization by foreign pollen. Neither does it as mother yield seed after being crossed with Central-European *C. varia*. The latter, however, produces hybrids with all other European amphimicts and at times also seems to be stimulated to self-fertilization.

This shows that *C. varia* in Gotland deviates from the normal

C. varia. The Gotlandic and Central-European *C. varia* have the same chromosome number, $2n = 28$. Probably the species has emigrated into Gotland during the subboreal period together with the several other species that have their home in Central Europe. Maybe a long isolation from the maternal population has developed a crossing barrier (cf. GULICK, 1905, pp. 6—7; DOBZHANSKY, 1941, chapt. VIII). In habitus the Gotlandic *C. varia* deviates from the Central-European, although the differences are slight. *Calamagrostis varia* from Gotland is not identical with *C. varia* investigated from Central Europe. It should therefore be given another name.

D. CALAMAGROSTIS ARUNDINACEA (L.) ROTH.
[Tent. II: 1 (1789), p. 89.]

This species, like *C. varia*, is assigned to the group Ancylatherae (characteristics: see *C. varia*). *C. arundinacea* is tufted, has long to very long genuflexed awns and as a rule a pale-green colour. It grows on moraines, preferably on the outskirts of woods [was once called *C. silvatica* (SCHRAD.) DC.].

C. arundinacea does not form ecotypes. The local variation covers so wide an area that two »sister-plants» from the same population are hardly more alike than plants from separate localities.

The species is very easy to recognize and as a rule its hybrids present no taxonomical difficulties. Among its distinctive traits the hairs between lamina and sheath constitute a reliable character. The genuflexed awns, which become double as long or more as the lemmas are more or less shortened in the majority of the hybrids, but are often absent in crosses with *C. canescens*.

E. CALAMAGROSTIS CANESCENS (WEBER) ROTH.
[HYLANDER, 1945 a, p. 76.]

This species is often confused with *C. purpurea*, which is an apomictic species. It will therefore be dealt with in connexion with the latter (p. 199).

2. APOMICTIC SPECIES.

A. CALAMAGROSTIS CHALYBAEA (LAEST.) FR.
[HARTMAN, Handb., ed. 4 (1843), p. 26.]

This species was described by LAESTADIUS from Scandinavia (Norway) as a form of *C. lapponica* (*Arundo lapponica*) in 1824 at the same time as TRINIUS set up the species *C. obtusata* on material from Central Asia (1824, Gram. unifl., p. 225). FRIES, 1843, raised LAESTADIUS's

form to a species (HARTMAN: ed. 4, p. 26). In that part of »Hartman's Flora» published in 1922 (HOLMBERG, p. 154) the name *C. obtusata* given by TRINIUS was also used for Scandinavian material. However, as *C. obtusata* from Central Asia is not identical with the type growing in Scandinavia, FRIES's name, *C. chalybaea*, ought to be kept for the latter.

C. chalybaea belongs to the group Ancylatherae set up by TORGES in 1898 (see HOLMBERG, 1922, p. 154). The most important characteristics of this group are the powerful, genuflexed awn issuing from near the base of the lemma and the woolly-haired transition between lamina and sheath.

C. chalybaea is hexaploid and has the chromosome number 42. The most interesting feature of the species is that it is apomictic and possesses a distinct connexion with both the Central-Asiatic *C. obtusata* and *C. arundinacea*. The latter species is amphimictic, and the same may be assumed to apply to true *C. obtusata*, which has excellent pollen of about the size possessed by tetraploid amphimictic species. *C. chalybaea*, however, never produces pollen.

In herbarium material Central-Asiatic *C. obtusata* seems to be slenderer in all parts than *C. chalybaea*. It differs from the latter species not only by its morphologically good pollen but also by its hairy leaves, which so far as is known to the present writer are never found in *C. chalybaea*. The Scandinavian apomictic species may have evolved from amphimictic *C. obtusata* through isolation from the mother population during the glacial period.

The possibility must not be ignored, however, that in spite of striking resemblances *C. obtusata* and *C. chalybaea* may have different origins. Studies of the public herbaria suggested this. In the Riksmuseum, Stockholm, there is material of *C. chalybaea* collected by ÖHRSTEDT at Ranåsbäcken in the neighbourhood of Östersund in 1916, 1918 and 1929. One of the sheets from 1918 shows a plant bearing a striking likeness to *C. arundinacea*. Especially the awns are of a length and an appearance that otherwise only occur in the last-mentioned species. The variation between the collections from different years is presumably due to different weather conditions. The present writer has himself observed in nature that *C. chalybaea* can show a very different appearance in separate localities. On cultivation in the same environment, however, plants from different places become perfectly like one another. It is therefore possible that the species is monophyletic in genesis, as NANNFELDT (1937, p. 9) has assumed for *Poa jemtlandica*.

Clonal plants cultivated in two separate fields a few hundred metres

apart but with different surface-water conditions were distinctly unlike. The differences concerned more especially the colour of the flowers. These were very pruinous in one field and approximated green in the other. Exposure to the sun was exactly the same in both cases. The modificative capacity of the species is thus great. This also applies to the development of hairs at the transition between sheath and lamina. Hairs occur here very distinctly in certain years but are almost entirely absent in other years in one and the same plant. The number of stolons varies very much in dependence on the weather during the spring.

The species occurs in nature preferably in the vicinity of water, along brooks, rivers, on wet meadowland, in bogs and similar environment. Consequently, the clayey soils of the experimental fields no doubt form an unsuitable substrate for the cultivation of this plant. *C. chalybaea* occurs in quite other natural localities than *C. arundinacea,* which grows in dry and sandy places. Hence the two species have different ecological requirements.

From comparative examinations of the two species the author has concluded that *C. chalybaea* cannot possibly be regarded as a hexaploid form of *C. arundinacea.* On the other hand, a plausible possibility is that it has arisen after a cross between the two amphimicts *C. arundinacea* and *C. canescens.* Comparison of *C. chalybaea* with hybrids between *C. arundinacea* and *C. canescens* showed that certain hybrid plants can hardly be distinguished from *C. chalybaea* (Fig. 199). The similarities embrace all the characters necessary for a determination. However, there are also some differences, e. g. the colour of the flowers at a late stage, the different tendencies of the panicle to contract after flowering, the degree of hairiness of the leaves, and so on. In these respects the hybrid plants are different.

As all the examined hybrids of the two species possess the chromosome number 28, while *C. chalybaea* has the number 42, there is a possibility that the species has arisen through fertilization of an unreduced gamete. Pollen tests showed that macropollen, presumably pollen grains with unreduced chromosome numbers, occur in certain *C. arundinacea* plants in a frequency of up to 2 %. One of the hybrid plants between *C. arundinacea* and *C. canescens* also possesses this type of pollen. It is not inconceivable that these or other types may produce unreduced gametes on the female side also.

C. arundinacea and *canescens* flower at the same time and are both tetraploids. When they meet in nature they almost unfailingly give rise

to hybrids. Such hybrids are common in certain parts of Sweden. The species have, however, different ecological demands, for *C. canescens* mostly grows in damp places. When it occurs in forests it is usually sterile. The two species therefore seldom have an opportunity of hybridizing in an environment suitable to both. Ecologically, *C. chalybaea* and *C. canescens* agree in that both grow in damp localities. Taxonomically, *C. chalybaea* is undoubtedly very close to *C. arundinacea*, and it was even interpreted by WAHLENBERG as a form of

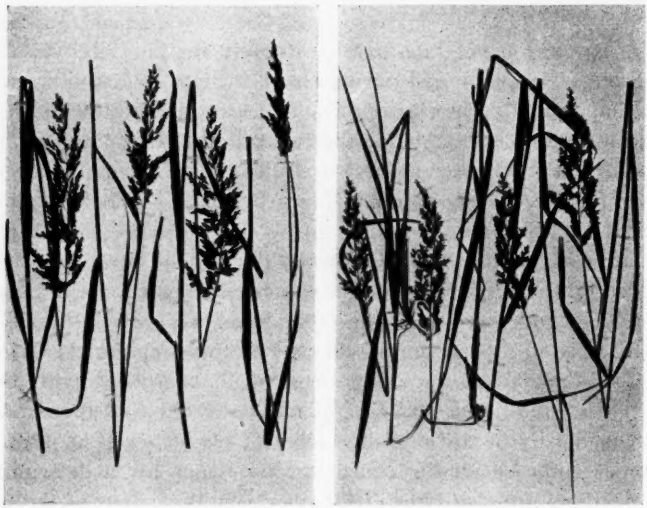


Fig. 199. To the right *C. arundinacea* × *C. canescens*, to the left *C. chalybaea*. The length of the sheets is 5 dm.

C. silvatica (SCHRAD.) DC. (= *C. arundinacea*). (See HARTMAN, 1843, p. 26.)

The species within the group Ancylatherae, in contrast to *C. canescens*, never form a branched straw. In the spring of 1945, however, a plant appeared in the I_4 of *C. chalybaea* that developed a lateral shoot from the axil of the basal leaf. The same property of forming branched straws is possessed by certain of the *C. canescens* hybrids with *C. arundinacea*, *epigeios* and *neglecta*. Variations occur in different years and at different seasons. The author interprets the lateral shoot that arose in *C. chalybaea* as a further indication that *C. canescens* may be contained in *C. chalybaea*. If this interpretation is correct, the apparent non-

occurrence of branched straws in the latter species would depend on the fact that the species contains four genomes from *C. arundinacea* and two from *C. canescens*. The two from *C. canescens* should then be »balanced» by the four from *C. arundinacea*, and therefore ramified types are either rare or only appear under certain exceptional external conditions. A hybrid obtained by the writer between *C. arundinacea* and *C. epigeios*, with two genomes from the former and four from the latter species, showed that in such cases the resultant plant may have an appearance that differs in essential features from the two parents. An effacement of the slight differences between the hybrid *C. arundinacea* × *C. canescens* and *C. chalybaea* is quite conceivable if the character of the entering chromosome set is altered.

The distribution of *C. chalybaea* in Scandinavia is such that the species may very well have arisen from *C. obtusata*, which during earlier geological periods may have had a more extensive distribution than now (HULTÉN, 1937, p. 116). At present *C. chalybaea* occurs, however, chiefly in western Scandinavia in a narrow belt between latitude 62 and 66. The species is common only in northwestern Jämtland and southwestern Lapland with neighbouring parts of Norway, although suitable localities are by no means missing in adjacent parts of the country. It seems to have spread to East Sweden along the river-valleys. In addition to this western range *C. chalybaea* also occurs in Imandra Lappmark. In Scandinavia its distribution coincides in the main with the northern boundary for *C. arundinacea*.

From what has been stated above it is evident that *C. chalybaea* may be conceived as arising in two ways, viz. either from amphimictic Central-Asiatic *C. obtusata*, which during the glacial period gave rise to an apomictic type, or through hybridization between *C. arundinacea* and, for instance, *C. canescens*. Which conception is the correct one may admit of being determined in a near future, as an octoploid *C. arundinacea* has now been produced by colchicine treatment, and crosses between such plants and different *C. canescens* types ought to enable the problem to be solved.

B. CALAMAGROSTIS PURPUREA (TRIN.) TRIN. AND CALAMAGROSTIS CANESCENS (WEBER) ROTH.

[Gram. uniflora (1824), p. 219. HYLANDER (1945 b), p. 446. — HYLANDER (1945 a), p. 76.]

The German *Calamagrostis* specialist TORGES set up in 1898 (p. 24) a group Homoeotricha. To this group belong four European species,

C. canescens (= *C. lanceolata*), *C. villosa*, *C. purpurea* s. str. and *C. Langsdorffii*. The last-mentioned species, however, produces transitional forms with *C. purpurea* and, in Europe, seems to be impossible or very difficult to distinguish from this. In eastern Siberia, however, *C. Langsdorffii* occurs as a quite distinct species, but in the Aleutian Isles and Alaska it develops transitional forms to *C. canadensis*, for which reason it is considered by HULTÉN (1942) to be a subspecies of the last-mentioned.

The species *C. canescens* was already known by LINNAEUS (= *Arundo Calamagrostis* L.; for the nomenclature, see HYLANDER, 1945 a, p. 76), while *C. purpurea* was described by TRINIUS in 1821 on material from Lake Bajkal (cf. LEHBERT, 1911). Originally TRINIUS called his species *Arundo purpurea* but altered this in 1824 to *Calamagrostis purpurea*. In 1832 HARTMAN described a Scandinavian *Calamagrostis* species under the name of *C. phragmitoides*. At the end of last century ALMQUIST combined the two species to one under the name of *Calamagrostis purpurea* TRIN. (LEHBERT, 1911, p. 1; NEUMAN, 1901, p. 769). The Esthonian *Calamagrostis* expert LEHBERT tried in 1916 to show that *C. phragmitoides* HARTMAN was in reality a hybrid between *C. purpurea* and *C. lanceolata* ROTH (= *C. canescens*) and well separated from the parent species *C. purpurea*. This view was maintained by LEHBERT (1930, p. 142), in as much as he considers HARTMAN's *C. phragmitoides* to correspond to *C. canescens* × *C. purpurea* forma *perpurpurea*. In earlier works LEHBERT vigorously defended the conception that *C. purpurea* and *C. Langsdorffii* were distinctly separated species, and a sharp debate on their specific values in the Linnean sense developed between him and LITWINOW. ALMQUIST suggests (1911) that a collective species, *C. purpurea* TRIN. coll., should be set up and that this should be divided into three subspecies: (1) *C. purpurea* (s. str.) TRIN. apud SPRENGEL, (2) *C. Trinii* ALMQUIST et LEHBERT (including intermediate forms), and (3) *C. Langsdorffii* LINK (= *Arundo Langsdorffii* LINK). These are in briefest outline the main features of the taxonomical history of *Calamagrostis purpurea*.

When the above data from the literature were supplemented by studies of herbaria the following facts could be elicited:

(1) *C. purpurea* is a species rich in forms and develops transitions to other species within the same group in the genus.

(2) *C. purpurea* forms hybrids with other species. At least one of these hybrids, *C. phragmitoides*, is assumed to have as extensive a range as the primary species, *C. purpurea*.

(3) There are transitional forms between different types within this group, which makes an objective estimation of the taxonomical position of different individuals very troublesome. Various specialists have energetically maintained diametrically opposite opinions of the same herbarium specimen.

The first step in the study of this taxonomically confused group was an endeavour to separate the large complexes contained in it from one another. It was found a simple matter to separate *C. canescens* and *C. purpurea* coll. All *C. canescens* plants in the experiments had hairy laminae, a character given in most of the floras. All plants belonging to this species also had the chromosome number 28, possessed a regular reduction division, excellent pollen formation, and failed to produce seed on isolation. *C. canescens* proved to be a good cross-fertilizing amphimictic species.

C. purpurea had as a rule smooth laminae and generally possessed longer ligulae and more luxuriant panicles than *C. canescens*. The chromosome number was 56 or higher, meiosis did not occur or was disturbed, pollen was almost without exception absent, and all plants produced seed after isolation. *C. purpurea* was a typical apomictic species.

The hairiness of the laminae varied considerably on the same plant year from year. On one occasion the writer had sent to him an almost glabrous *C. canescens* plant under the name of *C. purpurea*. When the plant was examined two years later it had hairy leaves. The next year, however, there was again a very sparse growth of hairs. Similar observations have been made in *C. purpurea*. In critical cases it proved simplest to separate slender *C. purpurea* plants from *C. canescens* by the pollen (LEHBERT, 1916, p. 18). Other methods also yielded excellent results, however. The nervation of the leaves is, in fact, different in *C. canescens* and *C. purpurea*. In *C. purpurea* the nerves are thicker throughout than in *C. canescens* (Figs. 202—205, p. 212). The number of nodes on the straw is a reliable characteristic in the majority of cases, being 4 or 5 in *C. canescens* but between 6 and 8 in *C. purpurea*. However, this may often vary in nature, the writer having found *C. purpurea* with 4—5 nodes in northernmost Sweden and in the experiments this character might vary from one year to another. The length of the ligulae is assigned great importance in the floras. Cultivation experiments with *C. canescens* and *C. purpurea* have shown, however, that young plants of the latter species seldom develop so long ligulae as old ones. LEHBERT's claim that the ligula in *C. canescens* is

only about 3 millimetres does not agree with the actual conditions: the ligula may be over 5 mm. long (cf. LEHBERT, 1916, p. 18). Nor does *C. purpurea* as a rule have a 10 millimetre long ligula as LEHBERT claims. His observations of the colour and shape of the anthers are very valuable, however. In *C. canescens* the anthers are X-shaped, purple and dehiscent, while those in *C. purpurea* are yellow and entirely enclosed in the floret. The thecae of the anther do not part in this species and the anthers are therefore I-shaped (cf. LEHBERT, 1916, p. 18; 1930, pp. 140—141). Originally the anther-colour character was demonstrated by ALMQUIST [1909, p. (65)], and therefore LEHBERT has presumably obtained this characteristic from him. ALMQUIST also draws an important conclusion from his find and says [p. (67)]: »The sterility of the anthers in *gracilescens* and *purpurea* may just as well depend on some kind of apogamy (as in cited *Taraxacum* and *Hieracium* forms) as on hybridity. The writer has never found anthers in any hybrid so perfectly empty as in *purpurea*, and as in *Taraxaca* and *Hieracia* they are» (translated from Swedish). It is remarkable that apparently the first to have noticed these extremely important lines, which were written almost 40 years ago, was STENAR (1932).

The characteristics may be summarized as follows: *C. canescens* is separable from *C. purpurea* by its well-developed pollen, its usually hairy laminae and their closer and slenderer nerves. It generally has a lower number of nodes on the straw than *C. purpurea*, 4—5 instead of 6—8. Both species may, however, show a certain amount of variation in these respects. *C. purpurea* in contrast to amphimictic *C. canescens* is an apomictic species. It does not develop pollen except in very exceptional cases — what LEHBERT (1916, p. 18) calls large-grained pollen are P.M.C's that have never undergone division. Such pollen mother-cells only occur in certain types and in these not in all florets. The anthers in *C. purpurea* are usually dry and withered and yellow in colour. When pollen is being examined in these species, the distal florets on the panicle branches ought never to be taken. As a rule they are withered and do not give reliable values.

After it had proved possible to separate *C. canescens* and its hybrids from *C. purpurea* coll. the chromosome numbers of different *C. purpurea* plants were arranged in the groups shown in the following table:

Table showing chromosome numbers in Scandinavian C. purpurea.

$2n$	56	± 63	± 70	± 77	84	± 91	
No. of clones ..	139	13	11	10	0	1	= 174

(A plant with $2n = 84$ was obtained in the crossing experiments. Such have not yet been found in nature.)

Determination of the chromosome numbers of the different *C. purpurea* plants rendered it possible to treat each chromosome-number type (or race) separately. The cytological examinations then undertaken showed that the same reproductive conditions prevail in all races independently of the chromosome number (diplospory with mitotic division). Any variations that occurred were probably due to the environment.

A taxonomical investigation of the types having high chromosome numbers revealed that just these plants possess certain traits reminiscent of the amphimictic species. Among these were plants with solitary leaf-hairs, which might be interpreted as a sign of affinity with *C. canescens*. Other plants had extremely short ligulae, 2—3 millimetres, others were unusually slender, while others, finally, were exceedingly thick with long well-developed panicles. As a rule they flowered somewhat later than plants with the chromosome number 56, but great variation could also be found in this respect. The further the examinations advanced, the more distinctly was it seen that these plants with deviating chromosome numbers must be considered to have arisen from octoploid plants, either through crossing with amphimictic species or through the ability of certain *C. purpurea* plants to produce pollen themselves.

Crossing experiments made during the years 1943—1944 between amphimicts and octoploid *C. purpurea* plants have shown that the conception advanced above must be correct (see p. 232). An interesting point, however, is that different *C. purpurea* plants behave differently in the crosses. The embryological investigation had shown that the egg-cell begins to divide at a late stage in this species. A fertilization would thus seem to be possible in a cross. Six *C. purpurea* clones having the chromosome number 56 were used as mother-plants in a number of crosses with tetraploid amphimictic species. In all cases the progeny had the maternal number of chromosomes (155 I-plants were chromosome-counted). Hence no hybrids had arisen. However, in view of the lability that characterizes the species it is conceivable that the same plants may produce hybrids another year.

In 1944 the previously mentioned *C. purpurea* plant from Gällivare, which had been thoroughly examined cytologically, was used as mother-plant in a large number of crosses. The chromosome numbers of the F_1 plants showed that in this case hybrids had arisen in the same

manner as was described earlier for *Poa* by ÅKERBERG (1939). If this *C. purpurea* plant, which has the chromosome number 56, is crossed with an amphimictic plant with the number 28, the progeny has the chromosome number 70 in the majority of cases. In some cases plants with the number 84 or thereabout arose, which must presumably be interpreted to the effect that in this case pollen from the *C. purpurea* plant itself had functioned on account of having been stimulated to self-fertilization by pollen from an amphimictic plant. These crossing experiments show that the writer's explanation of the occurrence of chromosome numbers above 56 is correct. An acceptable explanation is also obtained of the fact that these *C. purpurea* plants with the high chromosome numbers only occur here and there in nature in spite of the fact that *C. purpurea* and certain amphimictic species often grow side by side (*C. canescens* and *C. neglecta*). Their rare occurrence is attributable to the inability of the great majority of *C. purpurea* plants to produce hybrids. It seems as though a plant here and there of this kind constantly possesses this ability, while others are perhaps able to show a similar ability only in certain years.

Populations of such hybrid plants have been studied by the writer in Jormlien in North Jämtland and at Vilhelmina in South Lapland. In Jormlien a decaploid hybrid between *C. purpurea* and *C. neglecta* was spread over an area several kilometres in length. The type was very uniform and varied only very little in the different localities. The same applied to an undecaploid type at Vilhelmina.

The occurrence of races or hybrids with the chromosome numbers 63 and 77 suggest that reduced as well as unreduced embryo-sacs now and then function in *C. purpurea*. Another plausible explanation is that the nonaploids have arisen from primary hybrid plants having the number 42. Unreduced gamete plus reduced gamete would in that case give a nonaploid progeny. Hexaploid F_1 plants giving such an offspring have been produced artificially from the hybrid *C. arundinacea* × *C. epigeios*.

On cytological and taxonomical grounds the great majority of *C. purpurea* plants with high chromosome numbers must be regarded as species hybrids. It is, however, often difficult to determine these in the field. A hybrid with the number 70 contains eight genomes from *C. purpurea* and only two from the amphimictic paternal plant. Therefore, it is not very remarkable that as a rule these hybrids look like *C. purpurea* plants (for hexaploid *Phleum pratense*, see NORDENSKIÖLD, 1945). They can often, however, be distinguished from *C. purpurea* by

their gigas characters. Hybrids with the same chromosome numbers from different parts of Sweden sometimes were so similar that very probably they consisted of the same hybrid combination. This made it possible to divide the hybrids into groups and to obtain some conception as to which amphimictic species was to be regarded as father in the different combinations.

C. purpurea has the same ecological requirements as *C. canescens* and *neglecta* but may now and then be found along with *C. arundinacea* and *epigeios*. The present crossing experiments show that hybrids can be produced with at least *C. arundinacea*, *C. canescens* and *C. neglecta* forms. Types occurring in nature and considered to belong to these combinations have, however, often proved to have been wrongly determined. An instance of this is SAMUELSSON's description (1919, p. 250) of the hybrid *C. epigeios* × *C. purpurea* from Lövåsen in Darlecarlia. The type in question, however, is an unusually tall transgression form of the hybrid *C. canescens* × *C. epigeios*. It possesses pollen and has the chromosome number 28. Similar forms have been collected by LIDMAN in the Ljusdal area in Hälsingland (Riksmuseum herbaria). In this case it is a question of habitat modifications and shade types of *C. purpurea* ($2n = 56$). The hybrid *C. arundinacea* × *C. canescens* is often found in herbaria under the name of *C. arundinacea* × *C. purpurea*. This applies even to exsiccata issued (Riksmuseum). In the so-called *C. gracilescens* complex the conditions are at least as complicated, three different types occurring here, with the chromosome numbers 28 (= *C. canescens* × *C. neglecta*), 70 (= *C. purpurea* × *C. neglecta*), and 56 (= doubled 28-chromosomal hybrid).

What has caused the confusion in the determination of *C. purpurea* and its hybrids is the preconceived opinion that the hybrids are either intermediate between the parental plants or exhibit definite joint-characters from both of them. Hybrids with *C. purpurea* deviate, however, only slightly from the primary species. In most cases, therefore, one must be extremely sceptical when plants occupying a distinct intermediate position have been determined as hybrids of *C. purpurea*. As a rule hybrids between amphimictic species are concerned in such cases. A common argument advanced in support of the determination is that *C. canescens* is absent in the locality where the hybrid in question occurred. This frequently proves to be incorrect. For instance, *C. canescens* occurred plentifully in the previously mentioned locality at Lövåsen in spite of its non-discovery there by SAMUELSSON (1919, pp. 250—251). In the Karesuando area in northernmost Sweden both

C. canescens and *C. canescens* × *C. neglecta* occur despite the fact that at any rate the former has not been previously found there.

After it had been possible, thanks to the chromosome counts and pollen tests, to disregard these hybrid plants in the subsequent investigations, attention was focussed on *C. purpurea* plants with the chromosome number 56. At first sight these exhibit great heterogeneity, but this is only apparent, for they can be classified on quite new principles. As early as 1938 BABCOCK and STEBBINS (in earlier works as well) showed in America that certain apomicts having a high chromosome number within the genus *Crepis* are taxonomically associated with low-numbered amphimicts (as a rule diploids). In many cases it was also possible to show that the distribution of amphimicts and apomicts presented great similarities, i. e. that they had similar ecological demands. Within the genus there occurs what the authors have called an agamic complex. The same conditions prevail in the *C. purpurea* group, though here they are in certain respects more complicated. Some types here, in fact, connect on to amphimictic *C. canescens*, while others can be referred to hybrids between *C. canescens* on one hand and other Scandinavian amphimicts on the other.

The differences that occur between different *C. purpurea* types are habitat-determined to a high degree. Cultivation experiments show that certain dissimilarities are due to modifications, others are genotypically controlled. Progenies were raised from 40 different *C. purpurea* clones. These progenies were planted in groups of 12 plants, which enabled the variation of each type to be studied. The chromosome numbers of all these 40 × 12 plants were counted. It was evident from these counts that in none of the cases did the chromosome number of the progeny deviate from that of the maternal plants. In the majority of cases the progeny plants were morphologically very similar to the parent. In three cases the progeny varied somewhat irregularly, one plant in one number deviated very much from the sister-plants. In another experiment progenies were planted from isolated *C. purpurea* plants in rows of 39, 21, 25 and 35 plants. All the plants were also chromosome-counted in this case. No deviations in chromosome number from the parental plants could be discovered. One plant in the 39-group deviated distinctly from the sister-plants by slenderer leaves and lighter colour. This plant resembled *C. canescens*. In the two cases cited above true autosegregation (GUSTAFSSON, 1942 b, p. 269) could be demonstrated in these offspring. One of the maternal plants was from Säter in Darlecarlia and was planted out in 1938, the other was from Robertsfors in Väster-

botten and was planted in 1941. Personally the writer is inclined to consider these new forms as having arisen through formation of a restitution nucleus in a sexual E.M.C. that had been able to develop an embryo-sac on account of its unreduced chromosome number (DARLINGTON, 1932; GUSTAFSSON, 1934). These two cases show how new types can be formed even in an apparently obligate apomict (for *Rubus* compare LIDFORSS, 1907; for *Hieracium* see OSTENFELD, 1921).

These investigations thus made it clear that the polymorphy of octoploid *C. purpurea* has two causes: *a primary* heterogeneity is caused by its genesis, *a secondary* heterogeneity is caused by internal rearrangements of the gene-mass. The primary types thus become surrounded by a secondary form-series. The initial hypothesis set up by the writer was that the different primary form-series were derived from *C. canescens* and hybrids of this species with other amphimictic species. After comparative investigations of a large number of natural hybrids it was possible to distinguish the following four groups:

(1) One type that has probably sprung from amphimictic *C. canescens* through a doubling of the chromosome number.

(2) One type that has probably arisen through hybridization between *C. canescens* and *C. epigeios*. Respecting this possibility ALMQUIST wrote so far back as 1909 [p. (65)]: »And if we were not so accustomed to regarding *C. purpurea* as a species it would not at all appear to us so unreasonable to see in it *epigeios* × *lanceolata*: it is perfectly intermediate between these, in some forms rather like *lanceolata*, in others no less like *epigeios* . . .» (*C. lanceolata* = *C. canescens*) (translated from Swedish).

(3) One type which has probably arisen from the hybrid complex *C. canescens* × *C. neglecta*. Some of the forms belonging here have been interpreted by specialists as the hybrid *C. neglecta* × *C. purpurea* (= *C. gracilescens* BLYTT, partially).

(4) One type that has probably sprung from the hybrid *C. arundinacea* × *C. canescens*.

All these four form-groups may be expected to exhibit variations, even if solely on the ground that the primary material is heterogeneous. Coincident with the rise in chromosome number from 28 to 56 the forms have gone over to an apomictic mode of reproduction. *This is the cause of the preservation of the great primary variation.* Through apomixis the different hybrids that have arisen intra- and inter-specifically likewise become constant. As the variation of the primary species is enormous, a very great number of apomictic clones arise. This will be discussed later on in this paper.

Four apomictic *C. purpurea* types are illustrated in Figs. 200—201 together with corresponding amphimictic species or hybrids. All the *C. purpurea* plants possessed the chromosome number 56.

A *C. purpurea* plant from Boxholm in Östergötland one year possessed distinct leaf-hairs. The following year the hairs were missing. In

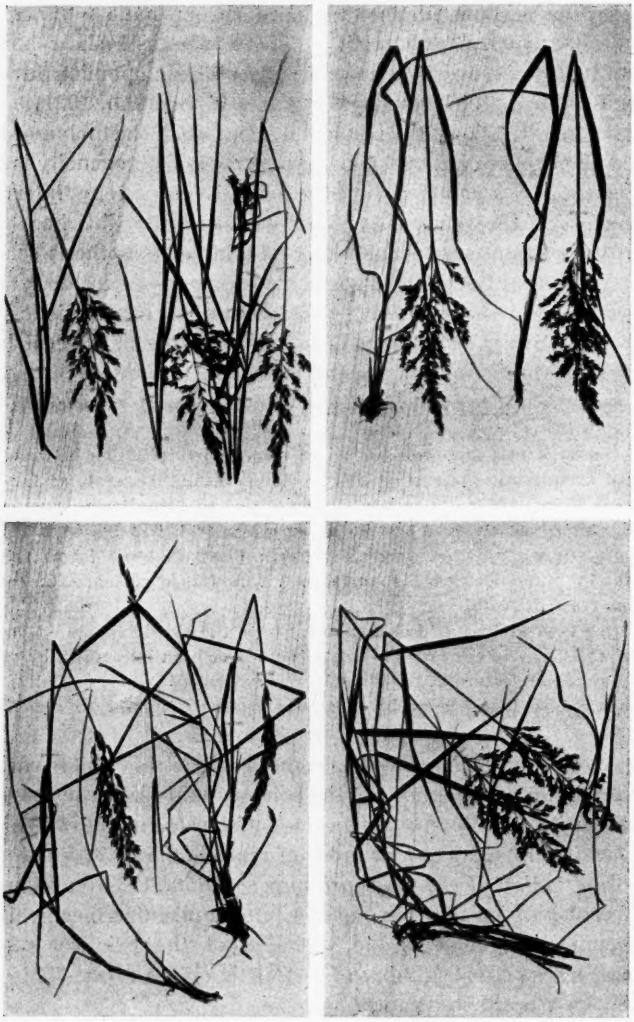


Fig. 200. From the left. Upper row, *C. canescens* $2n = 28$ and *C. purpurea* $2n = 56$. Lower row *C. canescens* $\times$ *C. neglecta* ($2n = 28$) and *C. purpurea* $2n = 56$. The length of the sheets is 5 dm.

this case it was only a question of a modification due to weather conditions. Earlier the writer had noticed some variation in different years

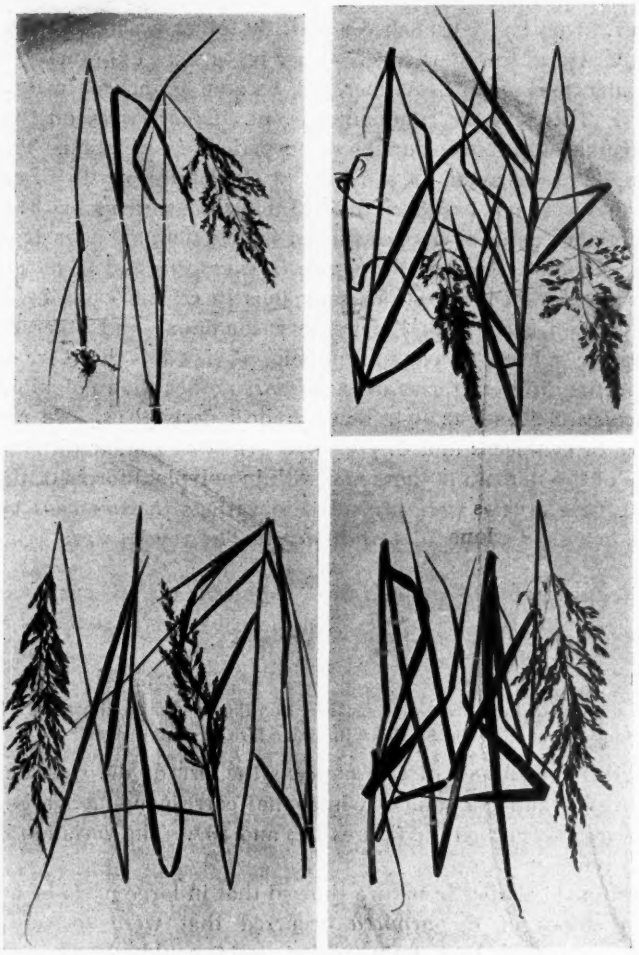


Fig. 201. From the left. Upper row, *C. canescens* × *C. epigeios* ($2n = 28$) and *C. purpurea* $2n = 56$. Lower row, *C. arundinacea* × *C. canescens* ($2n = 28$) and *C. purpurea* $2n = 56$. The length of the sheets in the lower row is 5 dm.

and seasons with regard to two other typical *C. purpurea* characters, viz. the length of the ligulae and the capacity of the species to form

ramified straws (cf. phenocopies; GOLDSCHMIDT, 1938). On the *C. purpurea* sheet in Fig. 201, upper row, there are two panicles, both from the same individual. The plant developed only these two this year. One has a branched straw, the other a simple one. They were collected at the same time. Other types were unbranched during the greater part of the summer but became branched towards late summer. This was the commonest event. Other types, on the other hand, remained simple during the whole period of vegetation. The same observations were made on a hybrid of *C. canescens* with *C. epigeios*. The plants were not branched in 1943, but they were so in 1944. The first developed panicles showed shorter ligulae than the later developed.

The characters which distinguish *C. canescens* and *C. purpurea* as well as their respective hybrids may thus in certain cases be entirely suppressed on account of the weather conditions and other external circumstances. From a taxonomical point of view it is therefore difficult to see in the different forms of *C. purpurea* other than polyploid types of *C. canescens* and its hybrids or hybrid derivatives. To ascertain whether *C. canescens* and *C. purpurea* exhibited similar differences in the size of the stomata to those met with in polyploid forms of the same species, these organs were measured in various *C. canescens* types as well as octoploid clones of *C. purpurea*. The results were as follows:

Measurements of stomata in C. canescens and C. purpurea.

Species	Mean (units)	No. of measured plants
C. canescens	8,9	12
C. purpurea	15,2	12

10 stomata of each plant were measured on the uppermost straw-leaf. The size of the stomata was found to be about the same also in other leaves.

In different plants of *C. canescens* the size of the stomata varies between 6,8 and 10 units, while the corresponding variation in *C. purpurea* is between the figures 14,3 and 16,5. The variation is slight in each type.

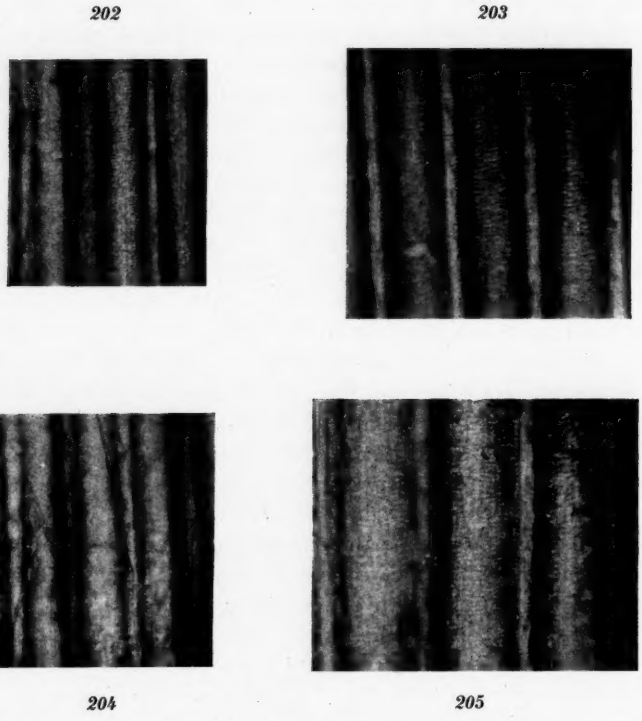
Continued studies in nature showed that in large parts of northern Sweden clones of *C. purpurea* occurred that were so confusingly like *C. canescens* that only pollen tests could determine which species was concerned. This type must be interpreted as a northern apomictic form of *C. canescens*. Careful investigations in Lapland showed that the hybrid of *C. canescens* with *C. neglecta* occurs in many places where *C. canescens* is to all appearances now absent. This has been taken by the writer as a proof that formerly *C. canescens* had a

considerably wider distribution in our country. Certain data for tetraploid *C. epigeios* point in a similar direction. If the view propounded here respecting the origin of *C. purpurea* is correct, the species may either have been formed in the localities where it now occurs or spread there from more distant-lying centres of formation. In this connexion it is interesting to note that DAHLSTEDT (1912, 1930) has arrived at the result that certain *Taraxaca* are glacial overwintering plants in Scandinavia, at the same time as K. JOHANSSON (1926, p. 327; see also 1923, pp. 196—197) has succeeded in showing that a number of *Hieracium* species with a limited distribution in Scandinavia arose after the Littorina period. ALMQUIST (1909) considers that *C. canescens* and *C. purpurea* invaded Sweden from the South and the North-east respectively. This is however hardly possible to prove, for *C. canescens* may very well have come from the North as well as from the South, the occurrence of *C. canescens* and its hybrid with *C. neglecta* at Karesuando pointing in this direction. Nor can the immense polymorphy that *C. purpurea* exhibits just in Scandinavia but apparently not in Russia and Siberia be explained if a small number had followed in the footsteps of the conifers from the East [ALMQUIST, l. c., p. (66)]. It is therefore probable that certain *C. purpurea* forms are glacial overwinterers or were formed during the interglacial periods, while others arose after the late glacial period. This question will be discussed below.

Full clarity as to the origin of *C. purpurea* can only be obtained by experiments. Forms having the chromosome number 56 may be produced from amphimictic *C. canescens* and its hybrids. This can be effected in two different ways, viz. either by colchicine treatment of seeds or direct by hybridization.

Seeds from a *C. canescens* plant from Östersund were colchicine-treated in the spring of 1944 (0,25 % solution; germinating seeds). Twelve plants with doubled chromosome number were obtained. These were sufficiently large for examination in the summer of 1945. All the plants have about three times as wide leaves as the original plant (10 and 3 mm. respectively) and are dark green in colour, while the original plant was light in colour. All the leaves on these plants possess the nervation typical of *C. purpurea* (Fig. 205) and are completely hairless. Their stomata average 15,3 units, while those of the original plant are 8,5. These twelve plants have not yet flowered, but *there is no doubt that they belong to the species C. purpurea and not to C. canescens.* An interesting feature in these cases is the disappearance of the leaf-hairs in a species solely because the chromosome number had doubled. As a rule

the dimensions of the various organs undergo a certain amount of change when the chromosome number is raised. Still, it is a very remarkable phenomenon that distinctly observable organs vanish because a plant has exactly doubled its original set of chromosomes. As all the twelve



Figs. 202—205. — 202, nerves of a leaf from *C. canescens* and 203 from *C. canescens* × *C. epigeios* (= synthetic *C. purpurea*). 204, the same from *C. canescens* (note the hairs) and 205 from *C. purpurea*, raised by colchicine treatment of seeds from *C. canescens* (Fig. 204). — Magnif. about 20 times.

plants behaved similarly in this respect, the disappearance of the hairs cannot be due solely to modification. In view of the fact that the plants were obtained through a doubling of the chromosome number in germinating seeds, they are very likely dissimilar, since *C. canescens* is a cross-fertilizer and very heterozygous. Presumably other *C. canescens* types that have undergone doubling of the chromosome number may

retain their hairs. The mother-plant used in this case has invariably developed hairs in culture during six years.

The possibility of producing *C. purpurea* by hybridization has also been realized. In this case a hexaploid *C. epigeios* plant was used as

Fig. 206. Synthetic *C. purpurea* ($2n = 56$), raised by crossing *C. canescens* ($2n = 28$) and *C. epigeios* ($2n = 42$). Plant height = 78 cm.

mother. This plant showed some tendency to form unreduced gametes in earlier crossing experiments. As *C. purpurea* has the chromosome number 56, one gamete from *C. epigeios* with the number 42 should unite with a reduced gamete from *C. canescens* in order to give rise to a plant with the number 56. This occurred in three crosses. In two of these an octoploid plant was obtained that could be identified without difficulty as *C. purpurea*. The third cross gave rise to five plants of the

same habit in a sterile condition. All seven plants have the chromosome number 56. One of these flowered in the summer of 1945 (Fig. 206). This plant, which is a typical *C. purpurea*, was isolated and produced seed. Unfortunately, these were infected with mould during germination. In the course of the summer, however, it was possible for the writer to see that this plant, like *C. purpurea* from nature, does not develop pollen. The leaves differ distinctly from those of the *C. canescens* plant used as father (Fig. 203). What is interesting in this case is the rather deviating habit of the plant from one of the parent species, *C. epigeios*. This is, however, a common phenomenon in the sexual species. In the experiments under review there is a hybrid between *C. canescens* and *C. epigeios* that almost entirely corresponds with *C. canescens*. The writer is inclined to consider that these cross-products which are so like one of the parents indicate that the different species within the genus are so closely allied to one another that initially all have arisen from one or a few primary species. Sometimes one, sometimes the other of the two hybridizing species can then set its stamp on the F_1 according to the number of dominant genes they introduce. Similar observations were made in the genus *Rubus* by LIDFORSS (1907) and in the genus *Salix* by HERIBERT NILSSON. Hybrids between *Salix cinerea* × *purpurea* and *S. aurita* resemble *S. aurita* to so high a degree that in nature they would be taken as large-leafed forms of this species (1930, p. 6). *Salix laurina* has arisen from the cross *S. viminalis* × *S. caprea* and not, as formerly assumed, from *S. phylicifolia* × *S. caprea* or from *S. phylicifolia* × *S. cinerea* (1928, p. 5). *S. cinerea*, finally, has also arisen from the hybrid between *S. viminalis* and *S. caprea* (1931). Thus, in the last-mentioned cases, *S. viminalis* is an integral part of *S. laurina* and *S. cinerea* without manifesting itself phenotypically.

It has accordingly been possible to synthesize *C. purpurea* in two different ways from amphimictic species with low chromosome numbers. *This should be regarded as proof that the species has arisen through inter- and intra-specific crosses in combination with polyploidy.* Whether the chromosome-doubled *C. canescens* plants will prove to be apomictic types is an open question. There would seem to be strong reasons for believing that certain plants within the species *C. canescens* and *C. epigeios* possess a tendency to apomixis and that this may be strengthened on an increase in the chromosome number. Other types, however, are presumably sexual even after doubling.

C. CALAMAGROSTIS LAPPONICA (WG.) HN.

[Handb. ed. 1 (1820), p. 46.]

C. lapponica possesses many points of resemblance to *C. neglecta* (THORSTENSON, 1893, p. 265). HOLMBERG sets up (1922, p. 153) a group Notatherae, which in Scandinavia and the Kola Peninsula comprises *C. lapponica* and *C. deschampsioides*. From Orthatherae, which includes *C. neglecta*, the group differs chiefly in the shape and placing of the awn. The awn should be straight in *C. neglecta* and more or less bent in *C. lapponica*. However, this character varies too much in the two species to play any part in a determination except in very clear cases, there being transitional forms. An examination of HOLMBERG's very detailed data respecting the distinguishing marks of the two species (pp. 152—153) shows that only two differentiating characters can be demonstrated that have not reference to pure quantitative differences: (1) callus hairs shorter than the lemma = *C. neglecta*; hairs longer than the lemma = *C. lapponica*; (2) leaves with thick, bristle-studded nerves = *C. neglecta*; upper surface of leaves somewhat sparsely thick-nerved, scabrous and often short-haired = *C. lapponica*.

On studies of the public herbaria the writer has found that in several cases *C. neglecta* has been placed as *C. lapponica* and *vice versa*, in both cases by good judges of the Scandinavian flora. These studies also clearly show that transitional forms exist, even if the conditions are by no means so chaotic as within the *C. canescens—purpurea* complex. That similar conditions also exist in other parts of the world was confirmed by an inspection of HULTÉN's flora of Alaska and Yukon (1942). He states, for instance, that a form of *C. lapponica* var. *brevipilis* has been referred to *C. neglecta* by the American grass specialist HITCHCOCK. Such misdeterminations are not likely to be made if there are no intermediate forms.

Studies of the two species in nature show that they possess the same ecological requirements. Certainly *C. lapponica* can grow in somewhat drier localities than *C. neglecta* and often occurs at higher levels in the mountains, but such differences are common between different polyploid races within the same species. Another observation is that different races of *C. neglecta* have corresponding ones in *C. lapponica*. In both there are tall grayish-green lowland species and short, very pruinous alpine forms. As a rule it is easy to distinguish them by the large flowers in *C. lapponica* and the hispidity of the leaves in *C. neglecta*.

The cytological and embryological analyses have shown that

C. lapponica is reproduced apomictically. The occurrence of pollen and occasionally of meiosis on the female side of this species furnishes at least theoretical evidence that sexual reproduction is possible. On the basis of the apomictic method of reproduction it is easy to explain the constancy exhibited by the local races of the species. The method of reproduction, however, gives no indication of the cause of the great similarity between certain races of *C. lapponica* and certain of *C. neglecta.*

The accumulated facts suggest that *C. lapponica—C. neglecta* constitute another branch of the agamic complex within the genus. Both the species are arctically circumpolar (see HULTÉN, 1937). (That *C. lapponica* has not been found in Iceland *may* depend upon failure to determine it or to observe it.) Thus, at Pajala in Norrbotten a *C. lapponica* type with strigous leaf-nerves has been discovered ($2n = 112$). At Kengis in the same district of Norrbotten a *C. neglecta* form ($2n = 28$) occurred with a broader or equally broad outer lemma corresponding to the most extreme forms in *C. lapponica.* This *C. neglecta* type also has solitary hairs on the nerves of the upper leaf-surface. Each of the plants thus exhibits a character typical of the other species. The occurrence of transitional forms with callus hairs of unequal length has long been known. A form set up by LAESTADIUS as *C. lapponica* var. *obtusior* (HOLMBERG, 1922, p. 153) has been regarded as a hybrid between the two species (according to herbarium specimens in the Riksmuseum, determined by several specialists). Chromosome counts of such plants have shown, however, that it is a question of a pure *C. lapponica* variety, a fact that need not imply that hybrids cannot be formed. *C. neglecta* from Yukon and Alaska has hairs as long as the lemma (Riksmuseum collections). In that region of the world there are also other species that do not occur in Scandinavia but that seem to bridge over the gap between *C. neglecta* and *C. lapponica* (e. g. the Alaskan race of *C. inexpansa* A. GRAY).

Counts made by FLOVIK (1938) and the present writer have shown that the chromosome number of *C. neglecta* is 28. As a rule, however, *C. lapponica* possesses very high numbers, as is indicated in the following table:

Table showing chromosome numbers of Scandinavian C. lapponica.

$2n$	42	49	± 91	± 98	± 105	± 112
No. of clones ..	2	1	1	4	16	29 = 53

The forms with a low chromosome number were collected at Porjus in Lapland. They were very much like *C. neglecta*, and had con-

siderably smaller florets than the other plants. They died in the field, however.

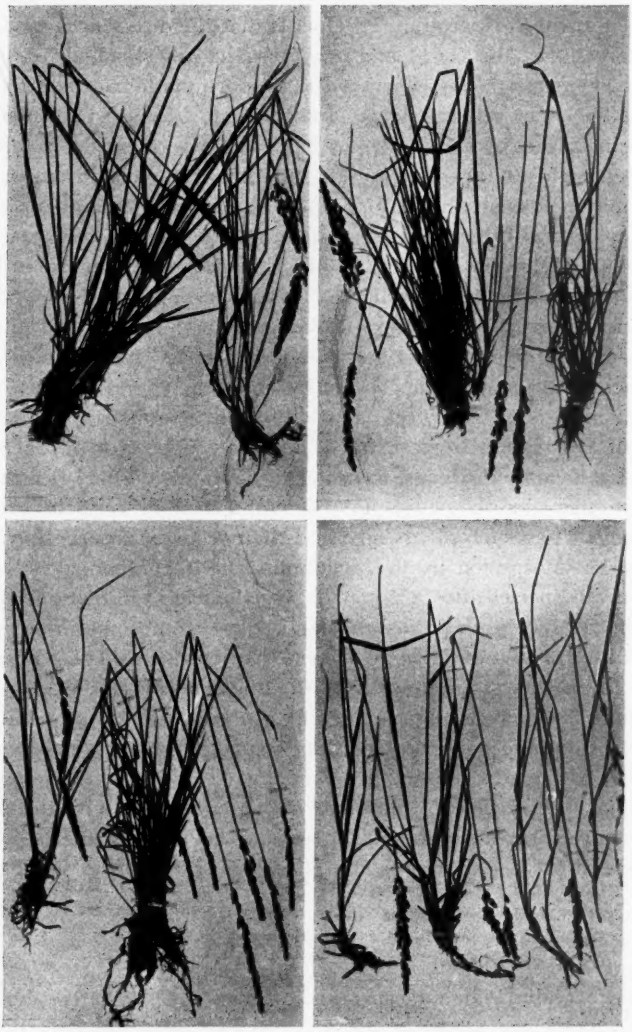


Fig. 207. From the left. Upper row, *C. neglecta* $2n = 28$ and *C. lapponica* $2n = 112$. Lower row, *C. epigeios* $\times$ *C. neglecta* $2n = 28$ and *C. lapponica* $2n = 112$. The length of the sheets is 5 dm.

The chromosome numbers afford an indication to the causes underlying the fact that the similarities between *C. neglecta* and *C. lapponica* are not so conspicuous as those between *C. canescens* and *C. purpurea* with the *C. canescens* group. The fact is that the differences in number are so great that the floral and other organs are changed to such an extent in the polyploid types that the proportions between the various parts of the plant are deranged. Intermediate forms, which constitute the missing pieces of the puzzle, are rare and have a limited distribution compared with the types having 28 and 105—112 chromosomes.

It may be asked why *C. lapponica*, like most of the other *Calamagrostis* species with high chromosome numbers, has not contented itself with octoploidy but has become 16-ploid (studies of pollen-size in Extra-Scandinavian *Calamagrostis* make it very probable that most of the species in the world have chromosome numbers about 28 or 56). No answer can be given to this question, but perhaps the phenomenon is associated with the extreme climate in which the species occur.

The meiosis in *C. neglecta* as well as pollen samples from different plants of this species suggest that it has the property of producing unreduced gametes. However, *C. neglecta* plants having another chromosome number than 28 have not been observed in spite of extensive searches. When such plants now and then occur in nature, they would seem to be interpreted by the taxonomists as *C. lapponica* or hybrids between this species and *C. neglecta.* Cytological examinations (p. 171) have shown that such plants as have a low chromosome number compared with the bulk of *C. lapponica* can also produce E.M.C's possessing double the chromosome number of the maternal plant.

There is much to suggest that *C. neglecta* does not constitute the only low-numbered type within this branch of the agamic complex. Fig. 207, lower row, shows a descendant from a hybrid population, *C. epigeios* × *C. neglecta*, that has a strong connexion with the strigous *C. lapponica* form from Pajala. It becomes even increasingly clear that there are also types that constitute a certain transition to the *C. gracilescens* complex.

3. CONCLUSIONS.

The Scandinavian *Calamagrostis* species form a heteroploid complex (BABCOCK and STEBBINS, 1938, p. 55). *C. varia*, however, possesses no connexion with other species. These may be divided into the following two groups:

A. Sexually polyploid complex (other species in Central Europe and in Asia):

C. epigeios group	*C. epigeios*	$2n = 28, 42, 56$

B. Agamically heteroploid complex:[1]

(1) *C. arundinacea* group	*C. arundinacea*	$2n = 28$
	C. chalybaea	$2n = 42$
(2) *C. canescens* group	*C. canescens*	$2n = 28$
	C. purpurea	$2n = 56$—91
(3) *C. neglecta* group	*C. neglecta*	$2n = 28$
	C. lapponica	$2n = 42$—112.

No sterility or crossing barriers occur between the tetraploids. Such may however occur in some cases, e. g. *C. varia* from Gotland.

Each of the groups (1)—(3) contains an apomictic species, while in the *C. epigeios* group polyploidy brings with it a transition to a special kind of self-fertilization (pseudofertility).

In spite of the fact that the development has to some extent taken separate paths within different groups the final results are alike. In one case cross-fertilizers have passed over to rather self-fertilizing types, in the other to forms with apomictic reproduction. So long as the cross-fertilizers with the low chromosome numbers are able to give rise to new polyploids it is perhaps a small matter which of the above-mentioned methods of reproduction is to be preferred for the derivatives formed. For, so long as these low chromosomal forms persist, evolution will go on and new amphimictic or apomictic polyploids will arise.

IV. EXPERIMENTAL INVESTIGATIONS.

1. ISOLATIONS.

Isolations were made on a large scale for the first time in the summer of 1941. Two or three panicles were isolated on the plants that had been placed out in the field in 1938—1939, all species being included, i. e. *C. epigeios* $2n = 56$ ten plants, $2n = 42$ three, $2n = 28$ seven, *C. arundinacea* eleven, *C. canescens* four, *C. neglecta* nine, *C. varia* three, *C. purpurea* twenty-six, *C. lapponica* three, and *C. chalybaea* three.

[1] It is clear from STEBBINS (1941, p. 527) that only one agamic complex per genus is assumed to occur. This is, for instance, evident from the data respecting the genus *Poa*. In the present writer's opinion at least every subgenus should possess its agamic complex. It rests however with STEBBINS to re-arrange this terminology and not with the present author. The writer's division of a complex into three groups must therefore be regarded as tentative.

As the seeds of *Calamagrostis* species are very small and provided with long hairs that make threshing both difficult and tedious, the florets of all the species that had been isolated were torn off when they had ripened and were sown out the following year in an unthreshed state. Of important numbers all florets with their seeds were sown.

Only from *C. lapponica*, *C. chalybaea* and *C. purpurea* were progenies obtained from all the isolated plants (p. 133). *C. neglecta* and *C. epigeios* $2n = 56$ gave, in contrast to other amphimicts, zero to five plants per number. It was however found that the apomicts also varied, some giving a copious progeny, others only solitary plants. In the years 1943 and 1944 a number of *C. purpurea* plants, together with one *C. lapponica* and three *C. chalybaea*, were again isolated. From each isolated panicle 200 florets were then taken at random. These were sown, as previously described (p. 133), and the number of plants arising was counted. The results proved to vary from year to year as well as with the age of the examined plants.

Table showing percentage of progenies from isolated plants of C. purpurea.

No.	J 4—*38* A	J 4—*38* C	S 1—*38*	S 2—*38* A	S 2—*38* B	S 6—*38*
1944	8 %	7,5 %	8 %	9 %	10,5 %	10 %
1945	9,5 %	9 %	8,5 %	9 %	11 %	10,5 %

No.	Dorot. 2—*41*	Jorml. 2—*41* A	Jorml. 2—*41* B	Klimpf. 2—*41* A	Klimpf. 2—*41* B	Källsta 1—*41* C
1944	2,5 %	8 %	6,5 %	2 %	2,5 %	3 %
1945	6,5 %	10 %	9,5 %	8,5 %	7,5 %	10 %

No.	Rob.-s 1—*41* A	Rob.-s 1—*41* B	Rob.-s 1—*41* C	Vansbro 2—*41*
1944	4 %	3,5 %	4 %	4,5 %
1945	6 %	7,5 %	7,5 %	12,0 %

No.	*C. lapponica* (same clone)	*C. chalybaea* (same clone)
1944	16	13
1945	17,5	13

The *C. purpurea* plants show an individual variation as well as a variation between plants of different age. The latter variation is rather wide; the 1938-year plants vary on an average only 8,47 % between the years 1944 and 1945, while the corresponding figure for the 1941-year plants is 109,9 %. This may be due to chance, but it may also be linked up with facts elicited from the examination of the mitosis and meiosis in panicles of different age. In 1943 the 1941-year plants developed

only one or two panicles per plant, while in 1944 they had grown strong and the number of panicles sometimes amounted to 100 or more. It is probable that in the summer of 1943 these plants produced a larger number of meiotic than mitotic E.M.C's. In that case it is quite natural that fewer seeds developed, as the meiotic E.M.C's would seem to possess only a small capacity to produce fully-developed embryo-sacs.

No tests were made of the germinability of the seeds. In the writer's opinion it is more important to know the number of plants developed per panicle than, for instance, the number of swollen seed-capsules. At the times the seeds were threshed before being sown the germinability was almost 100 %. Each panicle, however, seldom yielded more than a hundred or so germinable seeds, presumably owing to the panicle bearing so high a number of florets that the nutriment barely sufficed for all. Moreover, some flowers dry up under intense heat. The total number of seeds from an individual was, however, very large in spite of this reduction in seed production.

No great variations could be found for *C. lapponica* and *C. chalybaea*. It was noticed that plants of these species replanted at Svalöf from nature have difficulties in growing. The I-progenies raised from seed throve excellently, however. Among 20 *C. lapponica* plants raised, only one died in two years, whereas about 80 % of the old plants succumbed. No doubt the old plants found it difficult to develop roots to a sufficient extent. A not unessential cause may also be that the stomata of these plants were adjusted to a different climate than that prevailing at the experimental field.

2. CROSSING EXPERIMENTS.

A. METHOD.

After the isolation tests had shown that the Scandinavian *Calamagrostis* species were either amphimictic or apomictic, and that the former were self-sterile to a very great extent, a method was worked out for crossing. As it was conceivable that emasculation would prove to be unnecessary, an attempt was first made with isolating plants in groups according to the method used by WESTERGAARD (1943, p. 42). However, the great advantages of this method on the score of convenience proved to be counterbalanced by the disadvantage that after ripening the extremely light seeds of *Calamagrostis* species had a tendency to attach themselves to the panicle opposite that upon which they had originally developed. For this reason full reliance could not be placed on the results of the reciprocal crosses, and the method in question was afterwards used only when the reaction of one of the parents was known and when the object in view was to produce hybrid plants in as great numbers as possible. The crosses were then carried out so that panicles of the plants which were to serve as mothers in the contemplated crosses were isolated in great

number in early summer before the flowers had as yet opened. The panicles were thereupon isolated together with cut-off panicles from selected »male individuals». These panicles were placed alongside the »mother plants» in bottles containing water. In dry weather the »male panicles» had to be changed at least once a week. This method possessed the advantage that »male panicles» from early-flowering species (e. g., *C. neglecta*) could be taken at suitable stages in North Sweden and be sent to Svalöf, where the crosses were undertaken. In this way almost all combinations could be carried out without its being necessary to make them in the greenhouse, which affords a less suitable environment for the plants than the experimental field.

Both intraspecific and interspecific crosses were made.

B. CALAMAGROSTIS EPIGEIOS.

The crosses in this species were of two kinds:

(a) Intraspecific.

(1) Crosses within each chromosome race.

(2) Crosses between chromosome races.

(b) Interspecific.

In the first place the variation in chromosome number of the progeny was determined. As plants with different numbers are much alike in the germinal-bulb stage, the chromosome numbers of almost all the descendants were counted. In certain cases, however, only a preliminary determination or estimation was carried out, especially when the variation in chromosome number was small or none at all.

Results of crossings with octoploid C. epigeios as mother plant.

(a) Intraspecific.

Combination	No. of crosses	Chromosome numbers of the descendants									No. of plants	No. of chromosome-counted plants
		54	55	56	58	59	63	69	73	84		
56 × 56	8	1	1	107	1	2	1	2	1	1	117	106
56 × 42	6			51		1	1				53	53
56 × 28	12			146							146	146 estimated chromosome numbers.

(b) Interspecific.

Combination	No. of crosses	Paternal species	Species of progeny	2*n*	No. of plants	No. of chromosome-counted plants
56 × 28	11	C. a.	C. ep.	± 56	209	60
56 × 28	6	C. c.	C. ep.	± 56	100	100
56 × 28	6	C. n.	C. ep.	± 56	99	99

Abbrev.: C. a. = *C. arundinacea.* C. c. = *C. canescens.* C. ep. = *C. epigeios.* C. n. = *C. neglecta.*

These crosses show:

(1) That octoploid *C. epigeios* has not formed hybrids in intra-specific crosses. Respecting 56×56, see below.

(2) That *C. epigeios* $2n = 56$ has not formed hybrids with other species.

In crosses between two different octoploids descendants with varying chromosome numbers are obtained. Nothing else is to be expected, as the reduction division shows multivalents (p. 144).

Of the intra-octoploid crosses two were made between a hairy plant from Jämtland (J 3—38), which belongs to the variety called *paralis* Fr. in the floras and to glabrous types. In the cross having J 3—38 as mother the F_1 was hairy, while in that having J 3—38 as father it was glabrous. The cross-products between *C. arundinacea* (mother) and J 3—38 were hairy. A control of these peculiar crossing conditions was undertaken the following summer. A number of crosses were carried out with J 3—38 as mother and father alternately. Five of these crosses gave progeny, two of which with J 3—38 as mother and three with the same plant as father. In all cases the F_1 was of the maternal type. As J 3—38 was the only plant in the experiment which can serve as a »guide-plant» on account of its deviating appearance (which refers by no means only to the hairiness), it has not been possible to make the experiments on other material. In these cases self-fertilization is obviously present. Apomixis is excluded.

A comparison between intra- and inter-specific crosses with octoploid *C. epigeios* as maternal plant shows that self-fertilization had evidently occurred in all cases. These plants gave no progeny or only an insignificant one after isolation (0—5 plants per panicle). Abundant offspring were however obtained after a cross with amphimictic *Calamagrostis* species.

To ascertain what kind of pollen had a similar influence (cf. Winge, 1917, p. 242) a number of crosses were made in the summer of 1943 with »male panicles» from *Dactylis*, *Poa pratensis* and *Festuca rubra*. All the tests had a negative outcome. *Foreign Calamagrostis pollen thus stimulates to self-fertilization in the octoploid, while species-foreign pollen does not affect the seed-setting.*

Descendants of a cross between two octoploids varied very little (50 plants). Two plus variants and one minus variant arose, however, both with $2n = 56$ (Fig. 208). The two plus variants had 3 cm. broad leaves and a very robust habit, the minus variant was inferior to the

smallest of the tetraploids. The plant died after having developed panicles one summer. Such plants are probably eliminated in nature before they are able to develop panicles and multiply. Presumably, therefore, they have no rôle as primary plants for new forms. Feeble octoploids are occasionally met with in natural populations along with sister-plants of a fairly normal appearance. In some cases habitat modifications are then involved, in others minus variants of this kind play an obscure rôle. They often remain sterile.

Fig. 208. F_1 individuals from *C. epigeios* ($2n = 56$), raised by stimulated self-fertilization. The plant to the right is 116 cm. high.

WESTERGAARD (l. c.), working with Danish material, succeeded in obtaining a hexaploid F_1 in both the reciprocal crosses between tetraploid and octoploid *C. epigeios*. In the present investigation, however, where principally plants from northern Sweden were used in the crossings, F_1 individuals with the chromosome number $2n = 42$ were obtained only when the tetraploid served as mother. However, this need only mean that the materials in the different experiments were unlike. The variation within the species *C. epigeios* is so wide that it is quite possible for self-fertile, partially self-fertile and self-sterile plants to occur of the octoploid.

Results of crosses with hexaploid C. epigeios as mother plant.

(a) Intraspecific.

Combination	No. of crosses	Chromosome numbers of descendants															No. of plants	No. of chromosome-counted plants
		45	47	48	49	51	52	56	57	59	60	63	66	69	70			
42 × 56	1	2	1	3	1	4	1	1	1	1	1	1	1	1	1		20	20
		28	34	35	37	38	41	42	49	56								
42 × 28	1	12	2	2	6	3	1	4	1	1							109	32

(b) Interspecific.

Combination	No. of crosses	Paternal species	Species of progeny	Chromosome numbers of descendants	No. of plants	No. of chromosome-counted plants
42 × 28	1	C. a.	C. a. × C. ep.	35	1	1
			C. ep.	35—56	57	10
42 × 28	3	C. c.	C. p.	56	7	7
			C. ep.	35—52	64	10
42 × 28	3	C. n.	C. ep.	35—76	14	7

Abbrev.: C. a. = *C. arundinacea.* C. c. = *C. canescens.* C. ep. = *C. epigeios.* C. n. = *C. neglecta.* C. p. = *C. purpurea.*

The intra- and inter-specific crosses have given somewhat dissimilar results when hexaploid *C. epigeios* is used as mother. Concerning the mother-plants used in these experiments the following conclusions may be drawn:

(1) Hexaploid *C. epigeios* can form hybrids with other chromosome races within the species.

(2) With other amphimictic species hexaploid *C. epigeios* either forms hybrids or is stimulated to self-fertilization by foreign pollen. Species-foreign pollen gives a greater stimulance than species-specific.

The intraspecific crosses show that on being crossed hexaploid *C. epigeios* can give rise to forms with the chromosome numbers 28 and 56. This is very important, for from this finding it follows that evolution within the species may run from 28 over 42 to 56. This is probably the usual sequence of events. Hexaploids that are crossed with octoploids are able to give rise to new octoploids. A hexaploid plant occurring in a population of octoploids thus possesses the power to recombine, through a cross, different genes from these octoploids, even if these are themselves propagated through stimulated self-fertilization. The hexaploids play a large part in the genesis of new types within the species.

Of the interspecific crosses those with *C. canescens* are especially

important. *In three crosses here a new species has arisen*, viz. *C. purpurea*. The hybrids arose in all cases through an unreduced gamete from *C. epigeios* fusing with a reduced one from *C. canescens*. All the seven plants therefore have the same chromosome number: $2n = 56$. The same maternal plant was used with two different paternal plants.

Results of crosses with tetraploid C. epigeios as mother plant.

(a) Intraspecific.

Combination	No. of crosses	Chromosome numbers of descendants 28	34—38	42	No. of plants	No. of chromosome-counted plants
28 × 56	6	17		56	73	73
28 × 42	1	4	3	3	10	10
28 × 28	4	37		4	41	41

(b) Interspecific.

Combination	No. of crosses	Paternal species	Species of progeny	Chromosome numbers of descendants	No. of plants	No. of chromosome-counted plants
28 × 28	2	C. c.	C. ep.	28	47	10
28 × 28	3	C. n.	C. ep.	—	5	—
			C. ep. × C. n.	—	10	—

Abbrev.: C. c. = *C. canescens*. C. ep. = *C. epigeios*. C. n. = *C. neglecta*.

Tetraploid *C. epigeios* can be stimulated to self-fertilization by both species-specific and species-foreign pollen. Its apparently capricious behaviour is doubtless attributable to different plants behaving differently. Of the intraspecific crosses those between different tetraploids are the most important. In one case four hexaploids were obtained here as a result of isolating together two clonal plants from Röstånga in Scania. Only these four F_1 individuals arose from the cross in spite of the fact that the two co-isolated panicles contained about 1.000 florets. Maybe this can be interpreted thus that self-sterility can be abolished when an unreduced gamete functions on the female side (cf. YASUDA, 1933—1939). If the results of this cross are linked up with what was learnt earlier concerning progenies from hexaploid *C. epigeios*, full clarity is obtained as to the previously intimated course of evolution in *C. epigeios* 28—42—56. Octoploid *C. epigeios* is thus able to arise in a tetraploid population through crossing.

C. INTERSPECIFIC CROSSES WITH OTHER SPECIES THAN C. EPIGEIOS AS MOTHER PLANT.

(a) *C. arundinacea.*

Combination	No. of crosses	Paternal species	Species of progeny	Chromosome numbers of descendants	No. of plants	No. of chromosome-counted plants
28 × 56	3	C. ep.	C. a. × C. ep.	42	8	8
			C. a.	28	1	1
28 × 42	2	C. ep.	C. a. × C. ep.	35	3	3
28 × 28	2	C. c.	C. a. × C. c.	28	30	17
28 × 28	1	C. n.	C. a. × C. n.	28	16	5

(b) *C. canescens.*

Combination	No. of crosses	Paternal species	Species of progeny	Chromosome numbers of descendants	No. of plants	No. of chromosome-counted plants
28 × 56	2	C. ep.	C. c. × C. ep.	42	2	2
28 × 28	1	C. a.	C. c. × C. a.	28	27	27
			C. c.	28	15	15
28 × 28	6	C. n.	C. c. × C. n.	28	48	10

(c) *C. neglecta.*

Combination	No. of crosses	Paternal species	Species of progeny	Chromosome numbers of descendants	No. of plants	No. of chromosome-counted plants
28 × 28	1	C. a.	C. a. × C. n.	28	3	3
			C. n.	— over 20		—
28 × 28	3	C. c.	C. n.	27—31	68	27

Abbrev.: C. a. = *C. arundinacea.* C. c. = *C. canescens.* C. ep. = *C. epigeios.* C. n. = *C. neglecta.*

The hybrids that arose in the crosses between *C. arundinacea* and *C. epigeios* ($2n = 35$ and 42) are very like the latter species but are distinguishable from it by their genuflexed awn. As a rule, however, this does not project out of the floret as in *C. arundinacea.* The colour of the plants is the same pale green shade as is typical of *C. arundinacea.* One hexaploid hybrid changes appearance during the summer. During the first part of the vegetation period it resembles *C. arundinacea* to a remarkable degree, while later on it becomes more like *C. epigeios.* Above all, the appearance of the panicle varies. One of the pentaploid hybrids possesses very broad glumes. They are to some extent reminiscent of *C. lapponica.* Both the pentaploid and the hexaploid hybrid possess a more tufted habit than *C. epigeios.* The property the latter species shows of shooting long stolons in all directions is absent in the hybrid plants. Presumably, the hexaploid combination is very

rare, possibly yet entirely unknown in Scandinavia (Riksmuseum, collections).

The reciprocal crosses between *C. arundinacea* and *C. canescens* show that in at least these cases *C. canescens* must be genetically regarded as the dominating species. *C. arundinacea* did not come to expression in a single F_1 plant, whereas certain plants even with *C. arundinacea* as mother resembled *C. canescens*.

Table showing appearance of descendants after cross between C. arundinacea and C. canescens.

Combination	*C. canescens* appearance	Intermediate appearance	*C. arundinacea* appearance
C. a. × C. c.	4	8	0
C. c. × C. a.	4	23	0
Total	8	31	0

Forma per-*canescens* is far commoner in nature than per-*arundinacea*. Some F_1 combinations between the two species do not resemble either of the parents; quite new types may arise.

Of the crosses between *C. arundinacea* and *C. neglecta* those with *C. arundinacea* as mother resemble *C. neglecta* and are reminiscent of the type described by THORSTENSON (1893, p. 263). The three hybrid plants obtained in the reciprocal cross belong to the form-series per-*arundinacea*.

Crosses between *C. canescens* and *C. epigeios* are difficult to realize. This is due to the fact that the two species flower during different parts of the summer and therefore rarely have an opportunity of hybridizing in spite of their both having largely the same ecological requirements. It is therefore interesting to observe that this hybrid is rather common in the north part of Central Sweden and South Norrland. This is so because certain summers in these parts of the country favour a contemporaneous development of both species. If the flowering time of *C. canescens* is delayed, the chances of both flowering at the same time are increased.

This also applies to the formation of hybrids between, on one hand, *C. epigeios* and, on the other hand, *C. arundinacea* and *C. neglecta*. The hybrid of the latter species with *C. epigeios*, which has been described by HARTMAN, LAESTADIUS and WAHLENBERG under different specific names, the best known of which is *C. strigosa*, does not occur in Sweden south of Lapland more than in a few localities. The occurrence of the hybrid far up in Swedish, Finnish and Norwegian Lapland is a proof

that tetraploid *C. epigeios* possessed a far more northerly distribution formerly than is now the case.

The hybrid *C. canescens* × *C. neglecta* has formed one of the most difficult stumbling-blocks in *Calamagrostis* taxonomy. It was described in 1861 as a species *sui generis* by BLYTT under the name of *C. gracilescens*. Later it was found that this »species» consisted of at least two complexes — in reality it is a question of three: *C. canescens* × *C. neglecta* ($2n = 28$), *C. canescens* × *C. neglecta* ($2n = 2 \cdot 28 = 56$) and *C. neglecta* × *C. purpurea* ($2n = 70$). True *C. canescens* × *C. neglecta* ($2n = 28$), in contrast to the two others, always has pollen in the anthers, even if this may occasionally be of poor quality. In some parts of Sweden, especially in the Mälar counties, *C. gracilescens* is a characteristic feature in the vegetation, being group-forming in spite of its hybrid nature.

D. CONCLUSIONS.

These crosses between different amphimictic species in Scandinavia have shown:

(1) That no sterility barriers exist between them (except for *C. varia* from Gotland — secondary sterility barrier). The Central-European species *C. pseudophragmites*, *C. varia* and *C. villosa* are also crossable in all directions with the species described above. This fact — that all cross with all — is the cause of the critical character of the genus *Calamagrostis*.

All these species belong to the same *coenospecies* (TURESSON, 1922). Whether this is to be interpreted to the effect that they have a common genesis, cannot as yet be decided. Evolution has proceeded within the complex in different directions.

(2) The tetraploid form-circles are self-sterile, but this self-sterility can be abolished after stimulation by pollen from any amphimictic *Calamagrostis* species whatever within the area except from their own clone = pseudofertility. This property of self-fertilization increases in *C. epigeios* with polyploidy.

(3) It is probable that there are transitions between self-fertile and self-sterile types within the same species, likewise that the same individual as gives hybrids on being crossed with a species is stimulated by another to self-fertilization.

The occurrence of self-sterile and self-fertile plants has long been known. However, EAST and PARK (1917) showed that self-fertilization could occur in self-sterile *Nicotiana* species at the end of the period

of vegetation. This phenomenon was called *pseudofertility* by these authors. YASUDA has thoroughly studied the condition demonstrated earlier by EAST that in certain cases self-fertilization may be induced by dusting the pistil in young, unopened buds with pollen from their own plant. Self-fertilization does not take place at a later stage, which YASUDA explains as being due to certain substances that exercise an inhibitory action on the power of the pollen-tubes to push their way down into the style (YASUDA, 1933—1939 and lit. cited in these works). During the bud-stage these substances are not yet developed, and therefore self-fertilization can then take place. Pollen-tubes from foreign pollen are not arrested in their development.

In 1937 FAGERLIND showed that within the genus *Galium* pollen from another species could stimulate the pollen of a plant to self-fertilization (1937, p. 372). He obtained similar results from isolating diploid *Galium mollugo* and *G. verum* together as from doing the same with tetraploid and hexaploid *G. mollugo*. A very significant result, for it has recently been found that in many self-sterile plants with different chromosome races the diploid is usually absolutely self-sterile but the tetraploid only partially so or self-fertile. Tetraploids of this type occur, for instance, in *Tulipa*, where the tetraploid is completely self-fertile (UPCOTT and PHILP, 1939) and in oil turnip (= *Brassica campestris* f. *oleifera*), where the tetraploid is partially fertile (OLSSON, unpubl.). FAGERLIND showed, however, that the same diploid *G. mollugo* plants as had only given one seed in 964 fruits after isolation produced 127 seeds in 990 fruits after co-isolation. The corresponding values for the tetraploid were 158 fruits with 0 seeds without co-isolation and 184 fruits with 20 seeds after isolation along with hexaploid *G. mollugo* (FAGERLIND, 1937, pp. 373—374). All descendants were of the maternal type.

GUSTAFSSON studied in 1937 the sexual and extremely variable species *Taraxacum obtusilobum*. A comparison between isolated and freely-flowering individuals showed that the latter were about 1000 times as fertile as the former. The F_1 plants obtained after certain crosses reproduced the mother's type (GUSTAFSSON, unpubl.). Thus, in this case, it must be assumed that pollen coming from another plant had stimulated the plants to self-fertilization.

The form of pseudofertility set up by FAGERLIND is now known from at least three genera, viz. *Galium*, *Taraxacum* and *Calamagrostis*, in addition to which similar conditions also seem to prevail in *Veronica* (ZAMELIS and MELDERIS, 1931). It may be assumed that its occurrence

within three well-separated families in the vegetable kingdom means that this kind of fertility is more spread than has hitherto emerged in investigations of such phenomena. Its significance for the formation of forms and species within a genus is undoubtedly great.

As pointed out earlier, both *C. epigeios* and *C. neglecta* are very polymorphous in nature. Octoploid *C. epigeios*, however, deviates from tetraploid by producing distinct forms. Fruit is however developed only in the presence of other octoploid clone plants or another *Calamagrostis* species. This is the reason for HOLMBERG's statement (1922, p. 148) that fully developed fruit is no doubt very rare in *C. epigeios*. The writer has received the same impression from a study of *C. epigeios* in nature. Thus, the self-sterility described in this Chapter is not caused by the experimental arrangements, isolating bags, etc., but is a phenomenon known from nature.

E. CROSSES BETWEEN APOMICTIC C. PURPUREA AND AMPHIMICTIC SPECIES WITHIN THE GENUS CALAMAGROSTIS.

In the summer of 1943 six crosses were made between *C. purpurea* clones and the amphimictic species *C. arundinacea*, *C. canescens* and *C. epigeios*. These crosses gave rise to 156 F_1 individuals, which, except for two deviating plants, were all of the mother's type and possessed the mother's chromosome number, viz. $2n = 56$ (all progenies were chromosome-counted). Crosses were made in the summer of 1944 with the previously mentioned plant from Gällivare, which possessed the capacity to form pollen (p. 156). As paternal plants use was made of certain *C. canescens* forms, *C. arundinacea*, *C. neglecta* and the Central-European species *C. villosa* ($2n = 28$), which latter is closely allied to *C. purpurea*.

The embryological examinations have shown that this form of *C. purpurea* develops embryo-sacs according to the *Antennaria* scheme and produces triads after meiotic division in the E.M.C. These triads degenerate. There is a possibility that restitution nuclei may be formed and give rise to functional embryo-sacs.

These crossing results show as regards the mode of reproduction that there are two kinds of egg-cells in this plant, viz. egg-cells that are able to develop autonomously, and egg-cells that develop further after fertilization. The latter then give rise to descendants with the chromosome number 70 or higher (for the genus *Poa*, see HÅKANSSON, 1943). The cross with Bur 1—38 H makes it probable that both types of embryos occur in the same panicle. A third possibility is suggested by

Results of crosses between C. purpurea (2n = 56) and different amphimictic species having the chromosome number 28.

No.		Paternal species	No. of plants	Chromosome No. of descendants
G 1—41 × Trolleholm	1—41 A	C. c.	2	± 70
×	B	C. c.	6	± 70
× S. Rörum	1—41 A	C. c.	3	± 70
×	B	C. c.	1	± 70
× Kalmar	2—41	C. c.	2	± 70, 73.
× Linderöd	1—41 B	C. c.	3	48 (only one pl. determined)
× Innsbruck	2—41 A	C. v.	6	± 70 (4 pl.), 64, 68
× Järlåsa	4—41	C. a.	2	± 70
× S. 2—38 B		C. a.	1	± 70
× S. 14—38 A		C. a.	3	± 70
× Bur 1—38 H		C. n.	2	± 70, 56
× Dal 1—38		C. n.	7 (8)	± 70 (3), 75, 78, 80, 84, (42).
× S. 13—38		C. a.	43	56.

Total Hybrids + the I gen. 38 + 43. Varying numbers + 56

Abbrev.: C. c. = *C. canescens.* C. a. = *C. arundinacea.* C. v. = *C. villosa.* C. n. = *C. neglecta.*

the numbers 48 and 64 (the number 42 may be due to intermixture). In these cases egg-cells with the reduced chromosome number seem to have functioned. Such plants maybe possess but low vitality, for the plant $2n = 48$ died. The high numbers, 73—84, probably depend on self-fertilization.

All the isolated panicles were among the first developed by the plant that year. They were isolated long before the flowers opened. The first-developed panicles in this type gave more meiotic P.M.C's than mitotic (p. 182). The earliest panicles in these crosses produced only a few descendants per panicle. In all cases a fertilization of the egg-cell was required here to render seed-formation possible. The plants obtained were hybrids having the chromosome number 70 or direct offspring of *C. purpurea.* As the functioning female gametes were unreduced, there is the possibility that the seeds had arisen after formation of a restitution nucleus and that they originated from an E.M.C. that had undergone mitotic division. As restitution nuclei are apparently very rare within this clone, it is probable that mitotic division occurs and that the egg-cell in the embryo-sac formed according to the *Antennaria* scheme can be fertilized.

A study of the last »cross», where the egg-cell had obviously developed autonomously, shows that this »cross» alone gave rise to more descendants than the seeds from 14 panicles with formation of hybrids (two crosses duplicated). The number of plants are 43 and 38 respectively. Can there be clearer evidence to show how important the developmental stage of the flowers is?

3. ANALYSIS OF MORPHOLOGICALLY GOOD POLLEN AND POLLEN GERMINABILITY.

Only WESTERGAARD has previously studied the nature of the pollen in *Calamagrostis* (1943, p. 10). The paucity of data given in various floras probably depends on the fact that florets seated peripherally in the panicle have been examined. These are often dry and may be entirely destitute of pollen. WESTERGAARD has examined tetraploid and octoploid *C. epigeios*, four and six plants respectively of each. The octoploids had on an average 59 % good pollen and the tetraploids 91 % (100 pollen-grains were counted in all cases). WESTERGAARD does not give any information as to how these samples were taken. This is regrettable, as different methods may yield widely different results within this material.

Method. — A preliminary examination showed that pollen-tests made on crushed anthers did not give reliable results. This was no doubt due to the tendency of certain florets to dry up on hot days. The pollen tests included in this investigation were made on pollen obtained by isolation of panicles. These isolations were effected a day before the samples were taken. Germination of pollen was studied in a considerable number of florets. A solution was used of 3 % agar to which 14 % of cane sugar was added in distilled water. Drops of the agar were placed on the object-glass, encircled in a ring of vaseline and provided with a small piece of filter-paper drenched in water (DARLINGTON and LA COUR, 1942, p. 72). The pollen was strewn direct on the agar and a cover-glass was placed over in order to maintain the proper humidity. As a rule the temperature was about 20° C. After two days, acetocarmine was supplied to the preparation and the grains were counted. At least 200 pollen-grains from each number were counted. The samples were unfortunately somewhat irregularly drawn during the years, in certain years samples were taken from all plants available, in others from a part of the material. All the values for pollen germination are from the summer of 1945.

Percentage of morphologically good pollen from C. epigeios.

$2n$	Morphologically good pollen in classes								
	60 — 65	— 70	— 75	— 80	— 85	— 90	— 95	— 100	
28		1	0	2	4	8	9	9	= 33
56			1	6	6	3	15	4	= 35
42	1		1	2	1	1			= 6

M: 28 = 89,9; 56 = 87,6; 42 = 75,9.

The differences between tetraploids and octoploids are very small in these pollen samples, which maybe implies that the degree of polyploidy has less influence between, e. g., a tetraploid and an octoploid than between a diploid and a tetraploid. Structural differences in one or more chromosome sets are counterbalanced by other sets without defects. Some significance in this connexion undoubtedly attaches to the small number of multivalents in the octoploid, which conduces to stabilizing the chromosome number of the male gametes. The crossing experiments show that gametes with another chromosome number than 28 seldom function in the octoploid.

Different plants within the same natural population vary to a certain extent. This is evident from, e. g., ten plants from Gräsö in Upland.

Percentage of morphologically good and germinated pollen in C. epigeios 2n = 56.

No.	% morphologically good pollen	% germinated pollen	% germinated good pollen
Gräsö 1—43	92,9	64,3	69,2
2—43	90,6	67,8	74,8
3—43	91,4	65,1	71,2
4—43	92,0	56,7	61,6
5—43	85,9	57,3	66,7
6—43	90,1	50,0	55,5
7—43	92,8	56,7	61,1
8—43	93,2	66,3	71,1
9—43	82,4	44,4	53,9
10—43	89,3	59,5	66,7
M:	90,1	58,8	65,2

All the above-mentioned plants were examined in the summer of 1945.

A number of plants were examined that had arisen from »crosses», some between different octoploids, some between octoploid maternal plants and other chromosome races within *C. epigeios*. The content of morphologically good pollen was determined in 1944 and 1945, while the germination tests were made in 1945.

The plant with $2n = 58$ in »cross» 2—41 had low values in both years, viz. 70,5 and 76,5 respectively. Plants with $2n = 54$ and 84, however, had about 90 % good pollen. The previously mentioned minus variant (p. 223) had 67,5 % good pollen in 1944. In 1945 the plant had died.

Morphologically good and germinated pollen in »F_1 individuals» from octoploid C. epigeios obtained from »crosses» between different octoploid plants.

No. of cross	Chr. No. of descendants	No. of plants	% morphologically good pollen 1944	% morphologically good pollen 1945	% germinated pollen	% germinated good pollen
2—41	56 = 19 58 = 1	20	89,2	88,2	47,8	53,8
4—41	56 = 7 84 = 1	8	85,1	84,6	46,5	54,9
6—41	56	14	81,8	86,6	55,1	63,4
16—41	56 = 9 54 = 1	10	84,8	86,7	54,3	62,3

The variation within each cross is small. Values below 80 % in both years are only shown by three plants, disregarding the above-mentioned one with the chromosome number 58.

Morphologically good and germinated pollen in »F_1 individuals» from octoploid C. epigeios obtained from »crosses» between octoploid maternal and tetraploid or hexaploid paternal plants.

Combination	No. of cross	Chr. No. of descendants	No. of plants	% morphologically good pollen 1944	% morphologically good pollen 1945	% germinated pollen	% germinated good pollen
56 × 42	3—41	56	3	94,9	96,6	65,9	68,2
56 × 42	5—41	56	3	88,9	86,1	61,9	72,1
56 × 42	7—41	59	1	91,5	89,9	64,3	71,5
56 × 42	12—41	56 = 9 57 = 1	10	84,2	86,2	57,6	66,4
56 × 28	9—41	56	3	95,2	96,1	65,3	67,9

As the chromosome numbers show that self-fertilization must have taken place in this case, it is interesting to observe the difference between the plants and the high figures for morphologically good and germinated pollen.

The fact that the chromosome number itself has not so great a rôle in these plants is evident from the following list of F_1 plants between hexaploid and octoploid *C. epigeios*.

An interesting point is that the single octoploid plant obtained (No. 7) has poor pollen fertility compared with the plants that arose from various crosses with an octoploid mother. Cross fertilization can thus bring about the occurrence of new octoploids with more or less bad

Percentage of morphologically good and germinated pollen in F_1 individuals from a cross between hexaploid and octoploid C. epigeios.

No. of plant	2n	% morphologically good pollen 1944	% morphologically good pollen 1945	% germinated pollen	% germinated good pollen
1: 1	69	95,6	93,7	49,8	53,2
2	51	97,4	97,0	52,8	54,4
3	48	63,3	56,6	19,9	35,2
4	52	88,9	67,1	16,8	25,0
5	51	75,0	83,2	50,3	60,5
6	70	98,2	93,4	60,5	64,8
7	56	76,2	78,4	37,7	48,1
8	47	85,1	76,0	23,8	31,3
9	48	74,7	81,6	38,2	46,8
10	59	89,7	82,8	43,6	52,7
11	45	80,5	79,4	36,1	45,5
12	60	89,7	84,3	50,8	60,3
13	49	60,2	58,0	28,6	49,3
14	57	79,6	85,5	51,4	60,1
15	51	89,7	72,1	25,9	35,9
16	45	70,3	80,9	29,8	36,8
17	51	83,6	81,4	50,4	61,9
18	63	77,2	70,6	44,2	62,6
19	48	62,7	59,0	39,4	66,8
20	66	94,9	71,7	51,9	72,4
M:		81,6	77,6	40,1	51,2

pollen. Continued reproduction by self-fertilization within the clone ought to contribute to a general increase in this fertility through selection.

In spite of the extremely varying chromosome numbers in the above-mentioned hybrid plants the average of morphologically good pollen in a single plant for the years 1944—1945 does not fall below the average WESTERGAARD (1943, p. 10) obtained in an analysis of six octoploid plants (= 59 %). This must be attributed to differences in the material and to the fact that the chromosome number in itself does not mean so much in these plants. Different values of morphologically good and germinated pollen must depend upon the mutual states of balance between the chromosomes and structural or genic disturbances in solitary chromosomes or chromosome sets.

It is interesting to note the difference between the typical cross-fertilizers *C. arundinacea* and *C. canescens* and the partially self-fertile—pseudofertile *C. neglecta* (cf. MÜNTZING, 1939, p. 336).

Percentage of morphologically good and germinated pollen in C. arundinacea, C. canescens and C. neglecta during three consecutive years.

Species	Year	No. of plants with morpholog. good pollen in % 75	80	85	90	95	100	*n*	% germinated pollen (1)	(2)	Means All	Orig.
C. arundinacea	1943	1	2	1	1	11		16	—		93,2 %	93,2 %
	1944		2	2	9	9		22	—		92,8 %	92,7 %
	1945		1	6	9	6		22	36,9 %	39,0 %	91,5 %	95,9 %
C. canescens	1943	1	1	—	3	13		18	—		94,9 %	94,9 %
	1944	1	—	1	2	25		29	—		96,6 %	96,1 %
	1945	1	1	4	6	17		29	47,7 %	50,6 %	97,3 %	92,7 %
C. neglecta	1943					19		19	—		97,8 %	97,8 %
	1944					17		17	—		97,9 %	97,9 %
	1945				3	14		17	42,0 %	43,7 %	96,6 %	96,6 %

The two columns for germinated pollen are: (1) = germinated pollen-grains in % of total counted; (2) = germinated pollen-grains on number of morphologically good ones. Orig. mean = number of plants from which samples were taken all three years.

The crossing experiments have shown that after pollination with foreign pollen all these species can give rise to species-typical progeny through self-fertilization, though there is some interspecific variation in the strength of this tendency. All amphimicts, however, still retain the property of forming hybrids with one another in natural complexes. It is nevertheless to be assumed that the frequency of hybridizing will decrease to the extent the species become self-fertile. *C. neglecta* has almost reached the stage when, as mother-plant, it does not form hybrids because exclusively self-fertilization occurs. The species can practically only serve as a pollinator.

4. CYTOLOGICAL INVESTIGATIONS OF F_1 HYBRIDS BETWEEN DIFFERENT AMPHIMICTIC CALAMAGROSTIS SPECIES.

Investigations have been carried out to ascertain the course of the meiosis in a number of natural and artificial hybrids within the species. These hybrids can be divided into three groups, depending on their chromosome number: (A) Tetraploid hybrids ($2n = 28$). (B) Pentaploid hybrids ($2n = 35$). (C) Hexaploid hybrids ($2n = 42$).

A. TETRAPLOID HYBRIDS.

All the examined hybrid plants have a regular meiosis with 14 bivalents and a high content of morphologically good pollen.

Table showing meiosis and morphologically good pollen in different tetraploid hybrids within the genus Calamagrostis.

Hybrid	No. of plants	Meiosis Male side	Meiosis Female side	Pollen in %
C. a. × C. c.	14	14_{II}	14_{II}	74,9
× C. ep.	9	14_{II}	14_{II}	78,0
× C. n.	3	14_{II}	14_{II}	82,6
C. c. × C. ep.	7	14_{II}	14_{II}	65,5—92,0
× C. n.	4	14_{II}	14_{II}	67,0
C. ep. × C. n.	15	14_{II}	14_{II}	88,5

C. a. = *C. arundinacea.* C. c. = *C. canescens.* C. ep. = *C. epigeios.* C. n. = = *C. neglecta.*

A point worthy of note is that the meiosis, like the pollen, develops on the male as well as the female side exactly as in the pure species, a fact that supplies an explanation of the polymorphy within the genus. As the result of crossings between F_1 plants or of back-crossing with mother and father plants other or third-hand hybrids can be formed that are so perfectly like one or the other of the parental species that they cannot be kept taxonomically separate from this (p. 190). (For *Tragopogon*, cf. WINGE, 1938.) Genes from the foreign species obtained by crossing can doubtless contribute in certain cases to the occurrence of deviating forms.

B. PENTAPLOID HYBRIDS.

Of the hybrids with the chromosome number 35 only four plants have hitherto been studied of the combination *C. arundinacea* × *C. epigeios.* At meiosis trivalents and univalents occurred. One examined plant had 91,1 % morphologically good pollen in 1944 and 76,2 % in 1945. Of the pollen-grains 40,7 % had germinated in 1945.

C. HEXAPLOID HYBRIDS.

In a cross between *C. arundinacea* and *C. epigeios* $2n = 56$ from 1941 a hexaploid hybrid was obtained. Its peculiar appearance has been described earlier (p. 227). At an examination of the meiosis in this plant such great similarities with the apomictic species were discovered that it was necessary to examine both P.M.C's and E.M.C's very thoroughly.

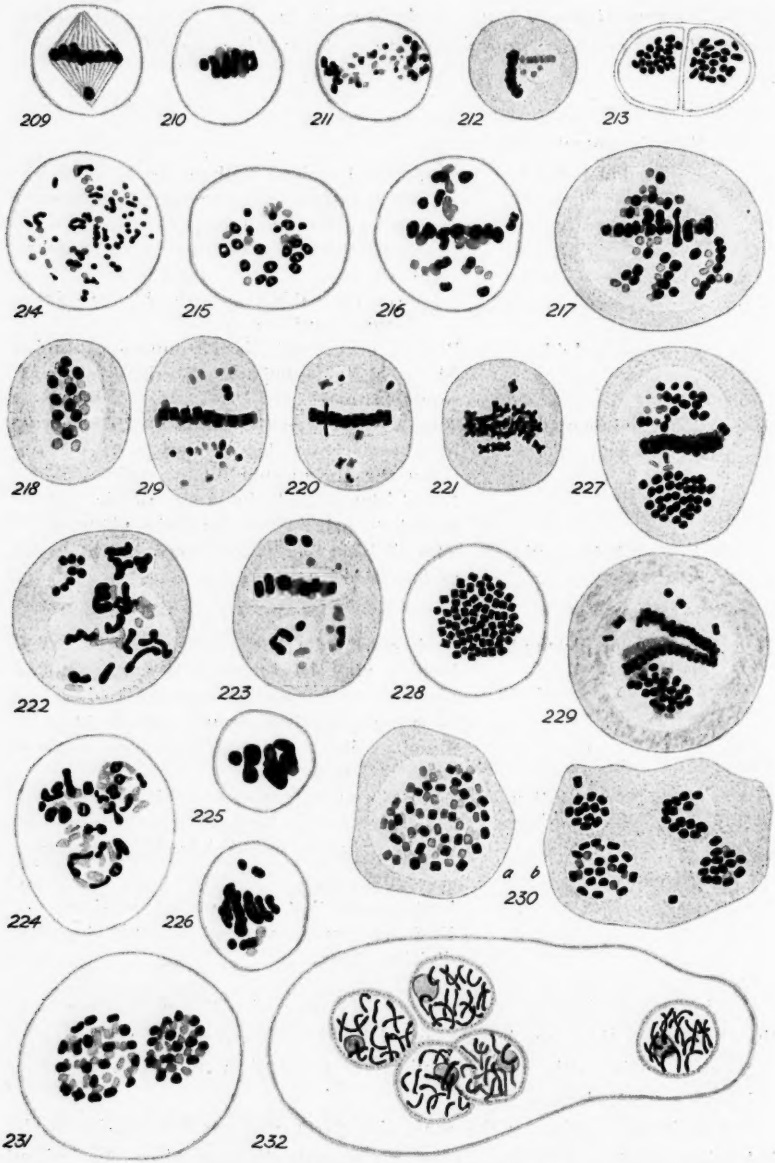
This examination has hitherto resulted in the following types of division being discovered in the pollen-mother cells.

Table showing different types of division in the P.M.C's of a hexaploid hybrid between C. arundinacea (2n = 28, mother) and C. epigeios (2n = 56, father).

I.	*Divisions occur.*	
A.	P.M.C's mutually free.	
	1. Normal P.M.C's.	(a) Normal meiosis with up to 21 bivalents. Very variable in number of univalents. Passes over into type (c). (b) Quadrivalents occur in small number, 1—3. (c) Asynaptic P.M.C's with 42 univalents. Forms transitions to (a).
	2. Synpolyploidy.	P.M.C's occur with the chromosome number 84 or higher numbers. Bivalents are only rarely formed.
	3. Pseudohomeotypic division.	This division type (GUSTAFSSON, 1935) occurs in a remarkably large number of P.M.C's. Often the chromosomes have divided at different times, and therefore all do not lie simultaneously in the equatorial plane.
	4. Semiheterotypic division.	This division-type is very rare, but occurs in certain P.M.C's.
B.	Plasmodia.	
	1. Fusion plasmodia.	Such plasmodia are common. The whole loculus may be included through disintergration of all walls between the P.M.C's. If divisions start, they usually only go on to the diplotene-diakinesis stage. Often development stops at leptotene.
	2. With restitution nuclei.	Such plasmodia are rare. Different chromosome plates often have different chromosome numbers and lie oriented in different planes.
II.	*No divisions.*	
A.		Resting cells that never undergo division.
B.		Fusion plasmodia without attempts at nuclear division.

The impression of immense lability given by the development of the P.M.C's in this type is intensified by the occurrence of sticky chromosomes, cells with several spindles, restitution nuclei, and other cytological disturbances.

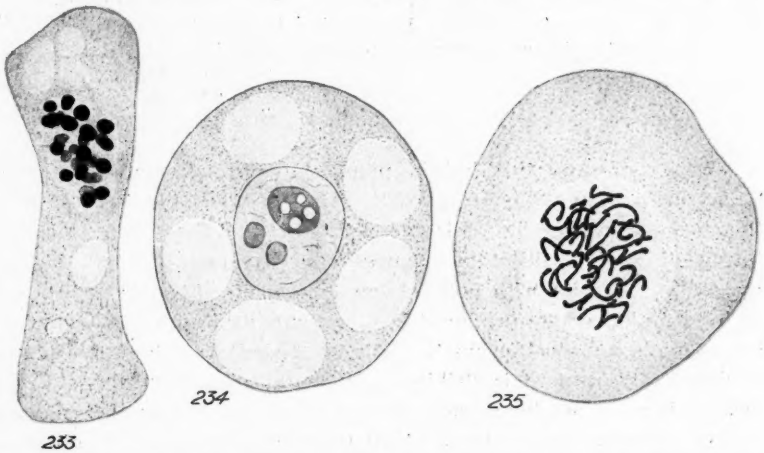
The irregularities on the male side prompted careful studies of the behaviour of the E.M.C's. After an examination of altogether about 2.500 flowers it was possible to determine that *E.M.C's occur with the*



Figs. 209—232. Hexaploid hybrid between *C. arundinacea* and *C. epigeios*. P.M.C's. — 209, first metaphase. 210, the same with a quadrivalent. 211, first anaphase with

mitotic type of division in this hybrid (Figs. 234—235; cf. STEBBINS, 1932). Four such cells have been observed, three in a resting stage and one in division (prophase). As a rule normal meiotic division occurs in the E.M.C's.

The occurrence in a hybrid of the mitotic type of division, so important for the reproduction of certain apomictic plants, supplies an indication of one of the paths taking by evolution in the genesis of apomictic species from amphimictic ones. Certain gametic combinations can obviously give rise to plants having such a physiological constitution



Figs. 233—235. E.M.C's from hexaploid hybrid between *C. arundinacea* and *C. epigeios*. — 233, meiosis. . 234—235, the mitotic type of division. Not all chromosomes drawn in 235. — Magnif. 950 ×.

that this, in interaction with definite environmental conditions, is able to bring about a mitotic division in certain E.M.C's while others retain the normal meiotic division.

A study of the progeny from this plant showed an unusally high percentage of plants with chromosome numbers above 42. The mother

split univalents. 212, second division (simultaneous) and 213 second division (successive). 214, first metaphase, the chromosomes start fragmentation. 215—216, the pairing varies. 217, a syndiploid cell. 218, semiheterotypical division. 219—221, pseudo-homeotypical divisions. 222—224, P.M.C's with their chromosomes in groups (syndiploidy). 225—226, »sticky chromosomes». 227, P.M.C. with metaphase-plates in different planes. 228, restitution nucleus. 229, as 227, formation of plasmodia begins. 230, plasmodium with chromosome groups of different size. 231, a »dyad» (gives rise to plasmodia). 232, plasmodium with 5 nuclei. — Magnif. 850 ×.

plant developed about 200 panicles in 1944. Only a few of these were isolated. No descendants were obtained from these panicles. On the other hand, 49 were obtained through free flowering. Standing some metres from the plant were *C. epigeios* $2n = 56$ and *C. canescens* $2n = 28$. These plants have apparently contributed with pollen in these crosses.

Chromosome numbers of descendants from hexaploid hybrid between C. arundinacea ($2n = 28$) and C. epigeios ($2n = 56$).

35	36	37	38	46	51	57	58	62	63	65	70	72	73	78	
6	4	9	2	1	2	1	3	1	1	1	12	2	1	1	= 47

Plants with a chromosome number above 42 = 55,3 %
» » » » » » 56 = 48,9 %
» » » » » » 63 = 38,3 %
» » » » » » 70 = 34,0 %

In its progeny this hybrid plant shows great similarities with *C. purpurea* from Gällivare (p. 232). That so many plants arose with the chromosome number 70 is due to the fact that these were probably formed through fertilization of an unreduced gamete from *C. arundinacea* × *C. epigeios* with pollen from *C. epigeios* ($42 + 28 = 70$), just as hybrid plants were produced in *C. purpurea* through fertilization of an octoploid unreduced gamete. The great similarity these two plants exhibit in this respect is striking — in both cases fertilization of the egg-cell is necessary for progeny to be formed. As the number of sown seeds of this type is very large, about 100.000, while the plants obtained were only 49, it is quite conceivable that the plant produced a certain percentage of E.M.C's that undergo mitotic division (about 0,16 %) but that these require fertilization in order to be able to give rise to an embryo.

As the hybrid plant in question is perennial, it can give rise, at any rate in certain years, to progeny having a strong tendency to diplosporous development. Apomicts with diplospory and mitotic division have presumably arisen from hybrid plants within more genera than *Calamagrostis*. The chromosome numbers of certain *Poa* apomicts point in this direction. However, this development does not exclude the possibility that the type of division in question may be formed in other ways. The occurrence of this division-type must be interpreted thus, that it depends on the genotypic constitution of the parental species. It can therefore by no means be expected that *all* hexaploid hybrids between *C. arundinacea* and *C. epigeios* develop mitotic division.

V. SOME CONCLUSIONS.

Within the genus *Calamagrostis* there are both amphimictic and apomictic species, the former being chiefly cross-fertilizers and mostly possessing a low chromosome number, while the hitherto discovered apomicts have chromosome numbers from 42 upwards. The apomictic species *C. purpurea* can occasionally form hybrids with the amphimictic species. In all examined cases these hybrids are apomicts and usually have the chromosome number 70. *C. purpurea* plants with $2n = 63$ are also known, however, but it is not very probable that these, like the former, are descendants of octoploid *C. purpurea*; presumably they descend from hexaploid plants. Synthetic *C. purpurea* ($2n = 56$), which has arisen out of a cross between *C. epigeios* ($2n = 42$) and *C. canescens* ($2n = 28$), had no pollen but nevertheless produced seed on isolation, just as *C. purpurea* does in nature, which points to apomixis in this hybrid.

A similar case is known from an investigation of the genus *Potentilla* by CHRISTOFF and PAPASOVA (1943). In a cross between sexual plants of *P. pennsylvanica* v. *sanguisorbifolia* and *P. adscharica* two apomictic F_1 plants were obtained. These authors assume that this was due to heterozygosis in the paternal plant, *P. adscharica*, and infer that within the genus *Potentilla* an apomictic mode of reproduction is dominant over a sexual one. This does not however accord with MÜNTZING's investigations within *Potentilla* (A. and G. MÜNTZING, 1941, 1945).

Apomixis may be manifested in an F_1 hybrid if disposition for such a method of reproduction is united in the zygote (SCHNARF, 1929, p. 546). Apomictic forms of *C. epigeios* and *C. canescens* are not known. Certain forms of *C. canescens*, however, connect direct on to *C. purpurea* in all morphological characters. In addition, typical *C. purpurea* ($2n = 56$) has arisen after colchicine treatment of seeds from *C. canescens* ($2n = 28$), and it must therefore be regarded as demonstrated that some *C. purpurea* types are autopolyploid *C. canescens* forms.

A strong indication of tendencies to apomixis in *C. epigeios* also is afforded by the fact that the mitotic type of division has arisen in the E. M. C.'s of a hexaploid hybrid between *C. arundinacea* and octoploid *C. epigeios*. Even though, in the examined cases, the embryo-sacs formed through this type of division only seem to have developed after fertilization, this need not mean that the plant is without the power of parthenogenetic reproduction. In normal apomictic *C. purpurea*, too, there occur embryo-sacs which to all appearances could not develop

without fertilization, in spite of the fact that most of them formed embryo-sacs by parthenogenesis. It is a well-known fact, indeed, that the mitotic type of division in apomictic species is associated with the occurrence of parthenogenesis, and hence this is presumably also the case with this »synthesized» type of division in a *Calamagrostis* hybrid.

All known hybrids between amphimictic species and *C. purpurea* are apomicts, which suggests that apomixis is a dominant phenomenon within the genus *Calamagrostis*, as it also is in *Hieracium* subg. *Archieracium* (CHRISTOFF, 1942). This is of interest because in hybridization between amphimicts and apomicts it seems to be normal for the progeny to be sexual, something that is evident from investigations in the genera *Rubus* (LIDFORSS, 1914; GUSTAFSSON, 1930, 1943), *Poa* (MÜNTZING, 1940) and *Potentilla* (A. and G. MÜNTZING, 1941—1945).

Various hypotheses have been advanced respecting the genesis of apomixis. According to STRASBURGER (1904, p. 158), there exists a connexion between apomixis and a weakening or complete loss of sexuality, so that difficulties in pollination and fertilization operate in a direction of apomixis. This hypothesis has been criticized by WINKLER (1908). WINGE considers that the apomictic species have arisen from the sexual through hybridization (1917, p. 200), a view that has been maintained more especially by A. ERNST (1918). WINGE's and ERNST's interpretation has met with criticism (WINKLER, 1920), and it has become increasingly clear of late years that *solely* hybridization cannot bring about apomixis (ROSENBERG, 1930; STEBBINS, 1941).

In certain cases a higher degree of polyploidy seems to operate in the direction of apomixis. DERMEN studied (1936) apospory in triploid *Malus hupehensis*. He found that polyploidy accelerates vegetative growth and decreases normal sexual development. In *Poa* autonomous development of the egg-cell occurred in hybrids resulting from the fertilization of unreduced egg-cells with reduced pollen, while such a development did not take place in hybrid plants that had arisen from two haploid gametes (ÅKERBERG, 1939, p. 366). HEILBRONN succeeded in inducing apogamy in diploid prothallia in *Polypodium aureum*, while this was not possible in haploid prothallia (1932). LEVAN produced a tetraploid hybrid between two diploid *Allium paniculatum* plants (1937). This hybrid was identical with *Allium oleraceum* and like this species was propagated by bulbils in spite of the fact that its diploid parents did not exhibit this type of formation.

That autopolyploidy *in et per se* cannot be considered to cause apomixis is evident from an investigation by KOSTOFF and TIBER (1939).

With the aid of colchicine they produced a tetraploid *Taraxacum Kok-Saghyz*. The tetraploid was sexual, like the diploid, although there are plenty of polyploid apomicts in the genus. CHRISTOFF (1940) came to the same result in the case of a doubling of the chromosome number of sexual *Hieracium leiophanum*, while a doubling of the number in apomictic *H. gothicum* gave a hexaploid ($2n = 54$), which, like the triploid primary plant, was an apomict and even showed the same type of division as this.

Some investigators consider that the form of polyploidy plays a significant part in the origin of apomictic species. THOMAS, for instance, in reference to the genus *Rubus* assumes that autopolyploidy is associated with apomixis, and allopolyploidy with a sexual method of reproduction (1940, pp. 125—126). This has however been shown by GUSTAFSSON to be erroneous (1943, pp. 113—115). FAGERLIND presumes that the agamospermous plants have arisen as intraspecific polyploids (1940, p. 42), something that does not agree very well with the observations BABCOCK and STEBBINS (1938) made within the genus *Crepis*.

Already in 1928 MÜNTZING succeeded in showing that diploid apomicts occurred within the genus *Potentilla*. This was confirmed later by POPOFF (1935). A diploid of this type has also been discovered by GENTCHEFF in *Hieracium umbellatum* (1941). It is therefore likely that within the plant genera containing apomictic species there are (a) diploids with manifest apomixis, (b) diploids with tendencies to apomixis, and (c) diploids without tendencies to apomixis. In crosses between diploids with tendencies to apomixis it is possible for apomicts to emerge. If such tendencies exist in several species within a genus it may seem as though hybridization, or in certain cases autopolyploidy, caused apomixis, whereas in reality only different genes that jointly produce this effect have been united in the hybrid zygote. Whether the zygote is diploid, autopolyploid or allopolyploid is in such cases a matter of complete indifference. Yet it is not excluded that certain genes possess different degrees of activity in, e. g., a diploid and a tetraploid that have arisen through chromosome doubling in this diploid.

FAGERLIND advances (1944 b, p. 194) the view that apomixis may often be a primary phenomenon, while polyploidy is a secondary one. As apomictic diploids are known, it is possible that such also occur in other genera than those mentioned above, but that they lead a languishing existence within their restricted range or have died out. As a matter of fact, it is known that polyploid types possess greater power of

resistance and adaptation than diploid ones. It is therefore quite possible that only the polyploid derivatives are extant, while the diploids have disappeared (for *Crepis*, cf. BABCOCK and STEBBINS, 1938). The peculiar conditions revealed by MÜNTZING in *Potentilla collina* (A. and G. MÜNTZING, 1943), and which also seem to occur in *Poa* (MÜNTZING, 1940; ÅKERBERG, 1942; KIELLANDER, 1942), make it theoretically possible, however, that diploid apomicts may have arisen from polyploid types.

From the above it is evident that no general rule can be formulated as to how and when apomixis appears in a genus of plants. Apomixis must nevertheless be interpreted as a secondary phenomenon, and sexuality as a primary one. The occurrence of a large number of agamic complexes within the vegetable kingdom (STEBBINS, 1941) shows that an apomictic method of reproduction occurs in many species within various genera in close association with amphimictic species. It may therefore be expected that such amphimicts in some cases possess genes for apomixis that can be manifested direct or in later generations through intra- and inter-specific hybridization in combination with polyploidy. The empirical data emerging from the investigations within *Calamagrostis* support this conception, for *C. purpurea* has arisen *both* after hybridization *and* after an increase of the chromosome number of *C. canescens*.

It should however be noted that the environment can affect a plant's power to multiply. The observations of the present writer within *C. purpurea* show that the same plant can occur as a facultative and an obligate apomict respectively in different years in the same environment. That a change of environment can cause similar effects is evident from LAWRENCE's investigations of *Deschampsia caespitosa* (1945).

Setting out from the assumption that amphimictic species are phylogenetically older than apomictic ones, it may be of some interest to examine the distribution of species with different methods of reproduction within a genus of plants. The genus *Calamagrostis* has spread to all parts of the world, but so far as it has been possible to determine by studies in herbaria (examination of pollen) apomictic species occur only in the Northern hemisphere in spite of the genus being especially richly represented in South America. Besides this, the apomictic species possess an Arctic-Subarctic distribution in the Northern hemisphere, while the amphimicts occur further to the South and only in exceptional cases in regions above the Northern Polar Circle (*C. neglecta*, *C. purpurascens* R. BR.). Three series of the agamic complex within *Cala-*

magrostis have been found in Scandinavia (p. 219), but in North America there would seem to be several such series. *C. inexpansa* A. GRAY is presumably apomictic on the Aleutian Isles and in Alaska, while in the more southerly parts of the Rocky Mountains it occurs as an amphimict. Thus, a distinct connexion is noticed within the genus between latitude and the occurrence of apomixis. Similar conditions appear to exist within certain groups of the genus *Taraxacum*, though our deficient knowledge of the geographical distribution of the many species within this genus does not permit of any general conclusions.

The amphimictic species *C. arundinacea* and *C. epigeios* are spread from West Europe up to West China and Manchuria. *C. canescens*, which is in many respects the most interesting species, is to be found from West Europe to the Altai Mountains (KOMAROV, 1934; HULTÉN, unpubl.). Of the Central-European species, *C. pseudophragmites* (the *C. epigeios* group) extends to the Himalayas and Tiensin, while *C. villosa* (the *C. canescens* group) occurs to Corea. *C. neglecta*, as previously mentioned, is circumpolar.

C. epigeios is maybe the youngest of the above-mentioned species. It is spreading more and more and occurs in, e. g., Africa, Kenya and in the Drakenberg Mountains and seems to have been introduced into North America (FERNALD, 1928). In Eurasia it is a common plant with an extensive range. It is the octoploid chromosome race that seems to be under expansion, and therefore this is obviously younger than the tetraploids, which are vanishing in many places. The experimental investigations have, in fact, shown that tetraploid *C. epigeios* can give rise to hexaploid F_1 plants and that hexaploid plants may possess octoploid descendants (pp. 225—226).

Of the apomicts, *C. chalybaea* seems to be endemic in north-western Europe. *C. lapponica* is easterly arctic, and *C. purpurea* is spread from Scandinavia to the Yenisei and Bajkal Lake. *C. Langsdorffii* TRIN., which in the region of transition is impossible to distinguish from *C. purpurea*, starts in North-Russia and Siberia. *C. canadensis* (MICHX.) BEAUV., which likewise produces transitional forms with *C. Langsdorffii*, commences in the Aleutian Isles and Alaska.

A close study of the power of *C. purpurea* to vary in different parts of its range suggests that there is the greatest wealth of types in Scandinavia. It is a well-known fact that a species is often richest in forms in the centre of its area of distribution (COWLES, 1901, p. 83; VAVILOV, 1928). A relatively short time has elapsed since the end of

those periods of glaciation which characterized the earlier phase of the Quarternary Age (RAMSAY, 1931). Hence, if Scandinavia is the centre of development for *C. purpurea*, this species either developed an abundance of forms in a short time after the last glacial period or else some of the *C. purpurea* types survived the glaciations in Scandinavia in ice-free areas or arose from amphimictic species during that period. As it must be considered practically impossible for all the forms of *C. purpurea* occurring just in Scandinavia to have arisen in the short period of time following the last glacial period, a combination of the possibilities indicated above is the most probable. A large number of Scandinavian species of plants survived the glacial periods in ice-free areas along the north coast of Norway. This must be regarded as a proved fact (see lit. in FRIES, 1913; NANNFELDT, 1935, 1940), and it may also be considered as established that some new species and forms were fashioned during this isolation. An example of this is offered by the genus *Taraxacum* (DAHLSTEDT, 1912, 1930). A new and very peculiar species of the genus *Calamagrostis* was discovered in the summer of 1945 at Pajala in northernmost Sweden, which may indicate the occurrence of very old elements of this genus.

C. purpurea occurs from most northerly Sweden down to Götaland, where it is rare (HÅRD AV SEGERSTAD, 1924, p. 171). The abundance of forms in the species is strikingly great from Darlecarlia up to southern Lapland. There is also a considerable wealth of forms in Norway, which is seen from the large number of »species» into which *C. purpurea* is divided there (cf. HOLMBERG, 1922, p. 150). This may be interpreted as indicating that within the area in question the species flowers at the same time as *C. canescens*, *arundinacea* and *neglecta* and in certain cases is able to form hybrids with these. None the less, it is a fact that the types with the chromosome number 56, i. e. not hybrids, are in greatest abundance in the part of Sweden mentioned above, which indicates that several *C. purpurea* clones have been formed just there. As only a small number of types would seem to have immigrated from the East, this generation of forms may not very well have taken place elsewhere than within the Scandinavian flora-area, since the species is entirely absent in Denmark and Central Europe. If primary stocks of the amphimictic species *C. canescens*, *arundinacea* and *epigeios* together with the hardy *C. neglecta* occurred in Scandinavia before the glaciations and survived these in refuges along the Norwegian coast, there have probably been numerous opportunities for new types or species to be produced as a result of mutual hybridization.

HERIBERT NILSSON has, for instance, synthesized *Salix laurina* SMITH (1928) as well as *S. cinerea* L. (1931) from hybrids between *S. viminalis* and *caprea*, besides which new *S. caprea* types have emerged (1918), while MÜNTZING has produced *Galeopsis Tetrahit* by means of a cross between *G. speciosa* and *G. pubescens* and a back-cross of this hybrid with *G. pubescens* (1930 b). Hence the original number of species need not by any means have been large for a new formation of species to have taken place in this way.

Some *Calamagrostis* hybrids can survive even severe external conditions on account of their capacity for vegetative propagation. Examples of this are hybrids of *C. neglecta* with *C. canescens* and *epigeios*. In Sylarna (Jämtland) of the Swedish alps *C. purpurea* occurs over 1.000 metres above the sea-level, and in many places in Torne Lappmark at a level of 800—900 metres. In the Norwegian alps it is found on Hardangervidda at a height of 1.400 metres (LID, 1944, p. 84). The species is sterile in all these cases, but in favourable years it can flower, at any rate in Sweden. For this reason hybrids formed in pre-, inter- or post-glacial periods were probably able to survive for a long time within their areas of formation by virtue of their vegetative power of propagation. In favourable summers they were able to develop panicles. It may be assumed that the repeated cold shocks to which these plants were exposed in the climate in which they occurred offered numerous opportunities for the formation of polyploid types. Among plants with a manifested apomixis, the polyploids gained ascendancy in the long run and were able to spread over large areas.

From what has been said it is evident that *C. purpurea* was able to survive the glacial periods even in fairly exposed localities. Some clones within the species can even reproduce themselves sexually (cf. the plant from Gällivare). Sexual *C. purpurea* probably had opportunities now and then of forming hybrids, amphimictic species having presumably immigrated from the East and South not only after the last glacial period but also during the interglacial periods. Certain *C. purpurea* clones may therefore have arisen from amphimicts which had invaded Scandinavia before the Quarternary glaciations, others are younger and were developed through mutual hybridization between amphimicts in the inter- or post-glacial period. The oldest types are presumably rich in obligate apomicts, while facultative apomicts may occur frequently among the younger forms (STEBBINS, 1941). Old as well as newly formed clones may be assumed to have hybridized, and to be hybridizing, with amphimictic species. Both *C. purpurea* and its

hybrids possess the power of developing new forms through autosegregation. The polymorphy within the species is thus due to the different *C. purpurea* clones being surrounded by a series of hybrids and derivatives of autosegregatives. Original clones as well as hybrids and derivatives are moreover very modifiable.

C. Langsdorffii and *C. canadensis* presumably occur as amphimicts as well as apomicts. Plants of both the species may possess excellent pollen or develop plasmodia of the same type as *C. purpurea*. In three clones of *C. canadensis* from Canada (collected by G. TURESSON) mitotic division has been found. The plants had the chromosome number 56. The same number was found in a *C. Langsdorffii* plant examined by the writer and which was likewise apomictic (locality unknown). Judging from herbarium material, *C. canadensis* (s. str.) varies slightly in comparison with *C. purpurea* (cf. STEBBINS, 1930, p. 41). HULTÉN arrived at the same conclusion after studying the species in nature. *C. Langsdorffii* bridges the gap between *C. purpurea* and *C. canadensis* and in the border-territory is impossible to distinguish from either of these.

Probably, the presumed parents of *C. canadensis* may have already invaded North America before the glaciations. East and west *C. Langsdorffii* attained contact with *C. canadensis* and *C. purpurea* respectively. Through hybridization between original amphimicts, or apomicts possessing the power of sexual reproduction as well, intermediate forms were developed. *C. canescens* may be regarded as a primitive type of the whole of this gigantic population, which in the Northern hemisphere is divided into three form-circles. In the Northern hemisphere this species probably had an extensive range in the Tertiary Period and succeeded in retaining life within a relatively large area on account of its property of vegetative propagation.

During the glacial periods different parts of this primary population were isolated in Scandinavia, Central Asia and North America. These three regions became the centre of development for *C. purpurea*, *C. Langsdorffii* and *C. canadensis* respectively, which is seen among other things from the wealth of forms of the respective »species» that occur just in these parts of the world. *C. purpurea*, however, also inhabits an easterly range. It is, for instance, described from Bajkal. This shows that evolution has followed the same direction in different parts of Eurasia, a circumstance that affords support for the view that the ancestors of the species had a more extensive distribution. It is conceivable that in the future *C. purpurea* forms will also

be discovered in North America. The three »primitive populations», which can be regarded as belonging to the same »Rassenkreis» (RENSCH, 1929), spread over extensive areas after the last glacial period, ran into one another in the border-regions and gave rise to the present distribution of the complex.

C. chalybaea is bicentric (FRIES, 1913, p. 318) in Scandinavia and in the Kola Peninsula. Possibly, it is to be found in North Russia. In Scandinavia it is confined to a relatively small, western range (p. 199). *C. chalybaea* is apomictic, while the closely allied species *C. obtusata* from Central Asia is amphimictic (pollen tests tend to show this). Within the range covered by *C. chalybaea* apomictic *Nigritella nigra* occurs (AFZELIUS, 1928, 1930), while sexual forms of this species grow in the Alps (CHIARUGI, 1929). There are also to be found within this part of Scandinavia several plants that possess a limited range here but have an extensive distribution in Central Europe, e. g., *Ranunculus platanifolius* and *Pedicularis Oederi* (TENGWALL, 1913). As the present distribution of *C. chalybaea* can hardly be satisfactorily explained (cf. p. 199) in any other way than that it is a glacial survivor, the fact is of interest that other plants which were evidently also isolated in Scandinavia during the glaciations occur in the same parts of Sweden as *C. chalybaea*. Whether the primary type was *C. obtusata*, or whether the species arose from the hybrid *C. arundinacea* × *C. canescens*, is difficult to determine; its present distribution argues definitely in favour of the species having a relict nature (HULTÉN, 1937, p. 116).

C. lapponica is poorer in forms than *C. purpurea*, but it develops several types that may often be referred back to the amphimictic species *C. neglecta*. Of its forms, *C. Holmii* LANGE has received the dignity of species, other forms such as var. *confinis* (WILD.) P. B. and var. *obtusior* LAEST. have been given varietal names. The three species *C. neglecta*, *C. lapponica* and *C. inexpansa* A. GRAY are close to one another. In many respects the last-mentioned seems to be intermediate between the two first-mentioned (see HULTÉN, 1942, pp. 165—166). The same applies to a new species collected at Pajala in northernmost Sweden. Mention was previously made of the fact that in Scandinavia *C. lapponica* possesses forms that are intermediate between this species and *C. neglecta*. *C. inexpansa*, however, suggests the occurrence of such intermediate forms in other parts of the world as well. Solely its extensive distribution suffices to give *C. lapponica* another position than the other apomicts. It endures an arctic climate and was therefore able to spread relatively early after the end of the glacial periods. Its

intimate connexion with *C. neglecta* and *C. inexpansa* suggests that this species-complex has undergone a development similar to that within the *C. canescens* group.

In the near future further results from the experimental work within the genus *Calamagrostis* will be reported. A taxonomical treatment of the Scandinavian and Eurasian *Calamagrostis* flora together with a phytogeographical investigation of the ecology of the Scandinavian species will be published later.

This work has been carried out at the Institute of Genetics at Svalöf, the Chief of which, Professor A. MÜNTZING, has kindly placed working space and staff at my disposal. To Professor N. HERIBERT NILSSON, Lund, I am very grateful for the interest he has shown in my work. To my friend, Dr. Å. GUSTAFSSON, Svalöf, I am very deeply indebted for discussions relating to various apomictic problems. From Professor H. GAMS, Innsbruck, and Dr. G. LOHAMMAR, Upsala, I have received interesting plant material.

I have had the benefit of thoroughly discussing certain sections of this investigation with Professors N. SYLVÉN, Källstorp, J. A. NANNFELDT, E. DU RIETZ and G. TURESSON, Upsala. Professor E. HULTÉN, Stockholm, has placed his profound knowledge of the arctic plants at my disposal. Drs. A. HÅKANSSON, A. LEVAN and H. SMITH have given me advice in critical cases. To these and many other unnamed advisers I beg to tender my best thanks for the assistance they have so generously given me.

SUMMARY.

(1) The grass genus *Calamagrostis* contains both amphimictic and apomictic species (p. 134).

(2) Of the following species, which have been found to be amphimicts, *C. arundinacea*, *canescens*, *neglecta* and *varia* are all tetraploid ($2n = 28$), while *C. epigeios* is tetraploid, hexaploid or octoploid.

(3) The amphimictic species are predominantly cross-fertilizers. Pseudofertility is nevertheless common. In crosses with species-foreign pollen progeny typical of the mother plant is obtained. The pseudofertility increases with polyploidy (p. 230).

(4) A hexaploid hybrid between the amphimicts *C. arundinacea* and *C. epigeios* ($2n = 56$) shows similar stages of division as the apomictic

species (p. 239). The mitotic division usual in the apomictic species occurs in E. M. C's of this hybrid. Examinations of descendants of this plant show that unreduced gametes occur.

(5) The species that on examination have been found to be apomicts are *C. chalybaea* ($2n = 42$), *C. purpurea* ($2n = 56$—91) and *C. lapponica* ($2n = 42$—112).

(6) *C. lapponica* occasionally forms pollen. Only 1 of 174 examined *C. purpurea* clones had this property. *C. chalybaea* does not develop pollen. Plasmodia are formed in the loculi of all three species, usually of fused P. M. C's.

(7) The meiosis is often disturbed in P. M. C's of *C. lapponica* and *C. purpurea*. In delayed P. M. C's of *C. purpurea* there occur, as in *C. chalybaea*, mitotic divisions. These divisions are preceded by a swelling of the resting nucleus (p. 161).

(8) Both meiotic and mitotic divisions occur in E. M. C's of the apomictic species.

(9) The development of meiosis and mitosis respectively in P. M. C's and E. M. C's of *C. purpurea* is influenced by external factors. In different years the same plant may form different percentages of cells with meiotic or mitotic division. The mitotic divisions are, however, always retarded in relation to the meiotic (p. 182).

(10) *C. purpurea* has been synthesized in two different ways. By colchicine treatment of seeds from the amphimictic species *C. canescens* ($2n = 28$) plants have been obtained that have the chromosome number 56 and that have been found to be identical with *C. purpurea*. By hybridization between *C. canescens* and *C. epigeios* ($2n = 42$) it has been possible to produce *C. purpurea* ($2n = 56$), in this case in three different crosses (p. 225).

(11) Apomictic *C. chalybaea* connects either on to amphimictic *C. obtusata* from Central Asia or on to the hybrid *C. arundinacea* × *C. canescens* (p. 196).

(12) Apomictic *C. lapponica* attaches itself to amphimictic *C. neglecta* and some of its hybrids (p. 216).

(13) *Calamagrostis* apomicts seem to occur solely in the Northern hemisphere. They possess an arctic-subarctic distribution.

(14) *C. canescens* is assumed to have had an extensive distribution in the Northern hemisphere during the Tertiary Period. During the earlier phase of the Quarternary of the glacial periods the primary population was isolated into three form-circles, from which *C. canadensis*, *C. Langsdorffii* and *C. purpurea* are assumed to have arisen.

(15) Apomixis within the genus *Calamagrostis*, at any rate so far as *C. purpurea* is concerned, has arisen as a consequence of intra- and inter-specific hybridizations in combination with polyploidy. It is probable that apomixis has also come to expression in other apomicts within the genus by the same method. The amphimictic species are assumed to possess genes for apomixis, which may be combined in a hybrid zygote. In itself the chromosome number is a matter of indifference, but it is probable that the activity of certain genes is intensified in a polyploid environment.

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CONTENTS.

I. Introduction 131
II. Cytological studies of Scandinavian species of *Calamagrostis* 135
1. Method 135
2. Mitosis 135
3. Meiosis 135
A. Amphimictic species 135
a. The male side 135
b. The female side 145
B. The break-down of meiosis in apomictic species 147
a. Terminology 147
b. Pollen mother cells 147
c. Embryo-sac mother cells 169
4. Embryology 175
5. Discussion of cytological results in the apomictic *Calamagrostis* species 177
III. Analytical studies of populations 186
1. Amphimictic species 186
A. *Calamagrostis epigeios* (L.) ROTH 186
B. *Calamagrostis neglecta* (EHRH.) 192
C. *Calamagrostis varia* (SCHRAD.) HOST 194
D. *Calamagrostis arundinacea* (L.) ROTH 195
E. *Calamagrostis canescens* (WEBER) ROTH 195
2. Apomictic species 195
A. *Calamagrostis chalybaea* (LAEST.) FR. 195
B. *Calamagrostis purpurea* (TRIN.) TRIN. and *Calamagrostis canescens* (WEBER) ROTH 199
C. *Calamagrostis lapponica* (WG.) HN. 215
3. Conclusions 218
IV. Experimental investigations 219
1. Isolations 219
2. Crossing experiments 221
A. Method 221
B. *Calamagrostis epigeios* 222
C. Interspecific crosses with other species than *C. epigeios* as mother plant 227

D. Conclusions 229
E. Crosses between apomictic *C. purpurea* and amphimictic species within the genus *Calamagrostis* 231
3. Analysis of morphologically good pollen and pollen germinability 233
4. Cytological investigations of F_1 hybrids between different amphimictic *Calamagrostis* species 237
A. Tetraploid hybrids 237
B. Pentaploid hybrids 238
C. Hexaploid hybrids 238
V. Some conclusions 243
Summary 252
Literature cited 254

THE EFFECT OF HETEROZYGOSITY ON VARIABILITY AND VIGOUR

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INTRODUCTION.

WORKING with progressive mutants in agricultural plants, the present writer wished to examine the effect of mutations, not only in the homozygous but also in the heterozygous condition. In most evolutionary discussions on mutations, their selective value has been judged from the homozygous appearance. It is generally conceived that a recessive mutation either shows no effect on viability in the single dose, or, if there is an effect, that the heterozygote directly reflects the properties of the recessive mutant.

Already here it must be emphasized that this idea seems to be entirely false. Certainly some reports on »monohybrid heterosis» have been published, with the heterozygote surpassing both homozygotes, one of which may be sublethal or lethal, but they have been ignored, or, if discussed, they are regarded as untenable. To take just two examples. In their text-book from 1939 STURTEVANT and BEADLE write (p. 276): »It is not probable that heterozygosis, *per se*, is responsible for the vigor.» Similarly MÜNTZING in his recent reviews of inbreeding degeneration (1943, 1945) contests the occurrence of a stimulance due to the heterozygous constitution: »Of the different inbreeding theories put forward the stimulance and plasmon theories» — advocated, for instance, by HERIBERT NILSSON, 1937 — »are still purely hypothetical and are not supported by any decisive experimental or cytological data» (1943, p. 247; translated).

The present writer has repeatedly come across cases where the heterozygote of chlorophyll mutations appeared to be superior to their normal sister-plants. In 1938 it was proved that they were never inferior, despite the completely lethal character of the recessives. A study of the literature has shown that the superiority of the heterozygote is fundamentally a demonstrated fact. Future investigations have merely to determine the frequency of these heterosis effects and to examine their general significance.

PREVIOUS RESULTS IN PLANTS.

The very critical experiment is to compare the heterozygotes and their normal sister-plants in segregating progenies of a mutation originated *in a pure line*. In fact, such a comparison has already been carried out by NILSSON-EHLE (1913) with regard to a chlorophyll factor in barley. The material available was small, but he found that there was no obvious inferiority of the heterozygote.

In 1927 RASMUSSON pointed out for *Pisum* that seeds harvested from plants heterozygous for the anthocyanin factor (*Aa*) germinated better than those harvested on the true-breeding purple-flowered *AA* plants or on the white *aa* recessives. Unfortunately, this important result was obtained after an F_3 analysis of crosses between highly different lines. The result cannot therefore be regarded as conclusive.

An ingenious kind of experiment was performed by MANGELSDORF (1928). He chose for investigation a mutation, destroying the normal embryo and endosperm development. Seeds homozygous for the mutation were small and shrunken, the embryos severely aborted and the endosperm soft and chalky. The mutation appeared in a highly inbred line of maize. In order to improve viability he crossed the line heterozygous for the lethal with another inbred homozygous strain. The F_1 generation possessed a genotype identical throughout, only the lethal appeared in heterozygous state in one half of the F_1 plants.

The height of the F_1 plants was measured on six consecutive dates. Owing probably to a smaller size of the seeds and embryos, the resulting heterozygous plants were shorter than the normals in the first two measurements. Finally the heterozygotes outgrew their normal sister-plants. The difference was not great (101 : 100). The length of heads was smaller in the heterozygotes (99 : 100). These were also somewhat later in ripening. The weight of their heads was 4 % lower than that of normal homozygotes. This very small decrease is surprising, considering that one fourth of the seeds are rudimentary, and that in addition some heterozygous seeds are probably inferior.

The first critical instance in which the heterozygote surpassed the normal homozygote was published by KARPER (1930). In a pure line of *Sorghum*, inbred for seven years, an *albina* mutant appeared. No doubt the mother strain was completely homozygous.

On five successive occasions KARPER measured the height of 380 individual plants in a segregating progeny. Of these plants 267 were shown to be heterozygous, 113 to be normal. In the first measurement

(after 20 days) there was a small preponderance of the homozygotes ($0{,}11 \pm 0{,}65$ [1] cm.), but in the next four measurements the heterozygotes were taller (final difference: $2{,}21 \pm 1{,}38$ cm.). Although the differences were not great, the heterozygotes appeared to be generally superior. This is also shown by the difference in plant and head weights at maturity ($32{,}3 \pm 20{,}7$ gms., $5{,}55 \pm 3{,}56$ gms. respectively). The length of the heads was somewhat greater in the heterozygotes. Heterozygotes produced suckers and side-branches to a larger extent than did the homozygotes. They were also earlier in booting and flowering. Summing up, they seemed to be visibly, although slightly, more vigorous than their normal sister-plants.

ROBERTSON (1932) made a comparative study of homozygotes and heterozygotes segregating for different chlorophyll deficiencies (three *albinas* and one *xantha*). Three of them were of the common type. The fourth one, which had arisen from »Canada Thorpe», gave extremely weak white seedlings, and the seeds poducing them could easily be picked out before planting owing to their small size (just half that of the normal seeds). Endosperm turned watery shortly after germination, at a time when it was still pasty in the sister seeds.

Of these four mutations one (a_c) showed consistent heterosis effects (Table 1). In all sets of measurements the heterozygotes were superior. This holds true of the total weight of kernels, number of kernels and number of culms per plant, but is especially manifest with regard to length of culms and heads. The P values indicate a pronounced effect. ROBERTSON says himself (p. 6): »The odds that such a difference would occur due to chance are over 22 to 1 indicating that the difference may be significant». In fact, the significance is much higher; for length of culm there is less than one chance in a thousand that the difference is fictive. The cited author points out, rather modestly, that there is no detrimental effect of the lethal-factor in the heterozygous condition (p. 12). Since the mutation was isolated in the »F_{11} generation of Colsess» (a hooded six-rowed barley), we may conclude that the heterosis effect is due to the heterozygous lethal itself, and not to closely linked growth-increasing genes.

In 1935 ROBERTSON and AUSTIN presented further material (one *xantha* and one *albina* mutation). The measurements of the a_{c3} heterozygote gave no conformal data. Probably there is a slight increase in height of culm. In the x_c heterozygote the heads of heterozygous plants were markedly longer than those of the homozygotes ($P < 0{,}001$).

[1] The probable errors, used by KARPER, have here been changed to standard errors.

TABLE 1. *Vigour of heterozygotes and homozygotes in barley.*
(Compiled after ROBERTSON, 1932, and ROBERTSON and AUSTIN, 1935.)

Mutation	Origin		No. of grains per plant	Grain weight per plant	No. of culms per plant	Length of culm	Length of head
albina$_c$	Colsess	1.	+	+	+	+ $P = 0{,}001$	+ $P = 0{,}01$
		2.	+	+	+	+ $0{,}1 > P > 0{,}05$	+ $0{,}05 > P > 0{,}02$
		[3.[1]	+	+	+	+ $0{,}05 > P > 0{,}02$	+]
xantha	Black Hulless	1.	−	+	+	− $0{,}05 > P > 0{,}02$	+ $0{,}05 > P > 0{,}02$
		2.	+	+	+	−	+
		3.	−	−	−	−	−
albina	Canada Thorpe	1.	+	− $0{,}02 > P > 0{,}01$	+	0	0
		2.	−	− $0{,}05 > P > 0{,}02$	−	−	−
albina	Hanna		+	+	+	−	0
albina$_{c_3}$	Colsess	1.	−	−	+	+	−
		2.	+	+	+	+ $0{,}05 > P > 0{,}02$	−
xantha$_c$	Colsess[1]		+	−	−	+	+ $P < 0{,}001$
Dihybrid	$a_c + x_c$		+ $0{,}01 > P > 0{,}001$	+ $0{,}01 > P > 0{,}001$	+	+	+ $P < 0{,}001$
Dihybrid	$a_{c_3} + x_c$		−	+	+	− $0{,}01 > P > 0{,}001$	−

+ indicates that the heterozygote is superior, − indicates that it is inferior.

[1] From crosses involving x_c and a_c.

The two authors also give some data relating to dihybrids. The double-heterozygote of a_{c3} and x_c is inferior to the green homozygotes, especially in height of culm. Consistently superior is the dihybrid of a_c and x_c. These two lethals taken separately increase vigour more or less when heterozygous, in contrast to a_{c3}, the heterozygote of which was indifferent with regard to vitality (except possibly for culm length).

Some objections may be raised concerning the test of the dihybrids. a_c and x_c are balanced lethals with only four percent crossing over. Therefore these double-heterozygotes cannot be compared with green homozygotes from the same offspring but from families segregating monogenically. Nor is it quite evident from ROBERTSON's original data on Colsess (1929) whether the head selections in F_{11}, giving a_c, a_{c3} and x_c, represent one and the same genotype. If Colsess I, II and IV are similar but not identical strains, the crosses between them do not afford a critical test [1]. In fact, ROBERTSON and AUSTIN (l. c., p. 440) suggest as a possibility that »the difference may be due to the recombining of dominant-growth genes linked with the lethal factor pairs in Colsess I and IV».

In 1938 GUSTAFSSON showed that induced chlorophyll lethals in pure lines of barley do not in any way decrease the fertility or the germination of the heterozygotes. His Table 8 (p. 60) shows rather that some of them increase the number of ripe seeds per head. *Alboviridis* X_2 (61 heterozygous and 22 homozygous ears) shows a relative figure of 111 to 100 with regard to seed number. Similarly 59 heterozygous and 19 homozygous ears of *albina* X_2 give a proportion of 111 : 100. In no case did the relative figure of the heterozygote fall below 95.

A mutation of great interest, further discussed below, is *xantha* 3. The heterozygotes apparently segregate very nicely according to 3 : 1 ($0{,}9 > P > 0{,}8$). It was found, however, that progenies from plants with a large number of ears showed a deficiency of recessives in contrast to plants having few ears. The dividing line was put down at five ears per plant. Plants with this or a smaller number were compared with plants having a higher number of ears and gave a difference with P less than 0,01. A mutation giving a general surplus of recessives was *alma alma* in *Antirrhinum majus* (p. 53).

In 1941 STUBBE and PIRSCHLE published a paper, which they

[1] Dr. ROBERTSON has informed the writer that these three F_{11} lines are phenotypically identical and most probably possess the same genotype. Colsess itself dates back to a single F_7 plant of the cross Coast × Success.

TABLE 1. *Vigour of heterozygotes and homozygotes in barley.*

thought to be the first one illustrating the superiority of the monohybrid heterozygote.

From the strain 50 of *Antirrhinum majus* PIRSCHLE obtained a mutation called *spectabilis*. It was unstable in homozygous condition, frequently mutating to normal in generative tissue or in late vegetative stages of development. The mutant was sublethal in homozygous state and caused a partial destruction of chlorophyll formation.

There seems to be no doubt that the heterozygote is more vigorous throughout than both homozygotes. This holds true of all essential vegetative characters: height, thickness of the stem, size of the leaves, height of the side-branches, and so on. The heterozygotes also develop more rapidly, the fresh and dry weights are higher and the total number of flowers is increased.

Consequently we must conclude that the authors are right in their statement of the increased vigour, caused by one factor in heterozygous condition. Moreover, the mutation in question functions as a sublethal when homozygous.

MÜNTZING (1945) has criticized this paper. He states that »the *AA* plants used for comparison with *Aa* and *aa*, do not seem to be derived from *Aa* plants but only represent normal plants in the *Antirrhinum* line in which the recessive mutant has appeared». The authors speak repeatedly of homozygous dominants. They do not emphatically state that these plants are segregates from the heterozygotes. This is, I think, rather obvious, however. Even *if* this should not be the case, it is equally interesting that a sublethal mutation that has arisen spontaneously and segregates monofactorially surpasses the original pure line when heterozygous.

MÜNTZING also attaches some importance to the fact that the *aa* genotype is unstable: »It does not seem clear that this change from *aa* to *Aa* only affects a single gene». *Aa* individuals segregate regularly according to 3 : 1. This would hardly be possible if meiotic irregularities or complex chromosome alterations were involved.

PREVIOUS RESULTS IN ANIMALS.

NABOURS and KINGSLEY (1934) report the finding of a lethal that causes death in the double dose (at a stage 4—5 days previous to hatching) but significantly improves the viability in the single dose, at least in juvenile stages of development. They further hold forth that »a principle of rather wide implication and importance may have come

to light through this discovery . . . we have been unable to find an account of a previous observation of exactly the same kind».

The lethal appeared in a stock of *Apotettix eurycephalus* and was traced back to an original female, with the smallest autosome chromosomes (chromosome 1) having the structure *Ymf*/*ZΘ*, and *le* lying in one of them, probably together with *Ymf*. After crossing over the chromosome *Ymf le ZΘ* was produced. Later on, the factors *T* and *G* were added. Thirteen different colour patterns are caused by dominant genes, closely linked and located on both sides of the lethals.

B
H
M
Y *G*
Ymf — *le* — *ZΘ* — *T* — *K*
0 2,95 6,9 7,4 7,43 units

Cross overs were experimentally obtained between *Ymf* and *le* and between *le* and *ZΘ*.

The lethal homozygotes make up 24 % of all eggs from the heterozygote, in close agreement with the expected value.

Crosses between animals heterozygous for the lethal gave a deficiency of dominant homozygotes ($0{,}01 > P > 0{,}001$), similarly the back-crosses of heterozygotes to normal homozygotes ($P < 0{,}001$). This fact proves that in any case the lethal-carrying part of the first chromosome increases viability when heterozygous. Certainly, the objection may be raised that the lethal lies extremely close to an unknown viability-increasing gene without any other effect. In such a case the lethal will be remarkably strong in homozygous conditions, and must entirely obliterate the effect of the homozygous viability-increasing gene. In the heterozygous state, on the other hand, the latter factor should predominate.

The heterozygous effect of the three factors *T*, *K* and *G* lying about four units to the right of *le*, was especially tested in back-crosses. In all instances there was a slight excess of heterozygotes but no significance. In addition, 58475 offspring from heterozygotes carrying various dominant colour factors, located in the first chromosome, were analysed and showed a very small surplus of heterozygotes (P was higher than 0,3).

These facts indicate that *the lethal itself* increases viability in single dose.

MASING's work on *Drosophila melanogaster* (1938, 1939 a and b) is very important.

Natural populations of this species (from Nikita Botanical Garden on the Crimea) showed a high number of lethals (22 %) in the second chromosome. The lethals were balanced in the laboratory with the aid of the *Cy* line (*Cy* acts as a lethal when homozygous; crossing over is reduced). The relative viability of flies heterozygous for lethals was studied in 32 cases. *Cy/le* males [1] were crossed with normal flies or with *ebony* flies (*ebony* lies in the *third* chromosome).

In the first experiment we should expect $\frac{+}{Cy}$ and $\frac{+}{le}$ to be formed in equal proportions. (That the chromosome-carrying *Cy* is also lethal when homozygous, does not interfere with the results.) Similarly, in the second cross experiment the ratio of $\frac{+}{Cy}\frac{+}{e}$ to $\frac{+}{le}\frac{+}{e}$ would be 1 : 1.

In eight cases (25 %) the lethals had a deleterious effect even in single dose, with and without *ebony* present. Two cases (6 %) showed a greatly increased viability in both sets of experiments. In three more cases (10 %) one of the two series gave increased viability. At least in 20 of the 32 studied lethals there was an effect, either positive or negative, in heterozygous condition. (In 1938 nine lethals out of nineteen showed a stimulation of the heterozygote.)

Of importance for a correct interpretation is the sometimes opposite behaviour of normal and *ebony* cultures with regard to heterosis. This was, for instance, the case in experiment 513 that gave 42 % flies having *ebony* in addition to the lethal chromosome, but in the normal cross gave 57 % flies with the lethal. Here *ebony* decreased the viability of the lethal chromosome. In other cases *ebony* increased viability of the heterozygous lethal, for instance, in experiment 518 that gave 62 % flies having both *ebony* and the lethal, as against 47 % flies in the normal series with the lethal alone.

All controls gave the expected ratios (1 : 1). Of 150 second chromosomes brought in from the same population but lacking lethals, none increased viability.

In order to test the viability adequately MASING crossed *Cy/le* males to females from the same population but carrying no lethal in the second chromosome. Controls were produced by crosses between these females and *Cy*/+ males. This latter series gave a surplus of *Cy*/+ flies (57 %, $P < 0{,}001$; the *Cy* chromosome works here as a stimulating lethal).

[1] MASING denotes the lethals with *l*.

In two cases out of 26 (8 %) the spontaneous lethals increased viability in the heterozygous state, and in eight cases (31 %) they decreased it.

MASING has carried the analysis one step further (1939 a). *Cy/le* males were crossed to females of the constitution *Cy/Bl L²*. Among other flies *le/Bl L²* females were also formed. These females were mated with normal males. Four phenotypes resulted: (1) normal, (2) *Bl L²*, (3) *Bl*, and (4) *L²*. Cross-over males (types 3 and 4) were crossed to normal females. If no lethal was present in the marked chromosome, the proportion of $\frac{+}{+}$ to $\frac{+}{Bl}$ or $\frac{+}{L^2}$ flies is 1 : 1. The occurrence of a lethal changes this ratio. Lethals, which increased viability in unaltered II-chromosomes, also produced the same effect in crossed-over chromosomes, whether they lay together with *Bl* or *L²*. In some crosses, however, lethals co-operated in a specific way with modifying parts of the same chromosome (cf. the crosses with *ebony*).

Two fundamental facts have come to light from MASING's experiments:

In many instances flies heterozygous for second chromosome lethals show increased viability. Spontaneous chromosomes without lethals never produce a similar effect.

The effect of the heterozygous lethal is modified by genes in other chromosomes (*ebony*) or by unspecified parts of the same chromosome.

MASING has attached some importance to his impression that the effect successively disappears in laboratory cultures. The specially published example (1938, Table 3) is not conclusive, however. In May, 1937, *Cy/le* × *+e/+e* gave a surplus of flies with lethals, D/m equalling 5,6. In November, 1937, the same cross gave a D/m equal to 3,4. A comparison of the two sets of data gives a P value of 0,3, i. e. the two cross experiments agree nicely with one another. Nevertheless, MASING's idea of modifying factors, which secondarily decrease the effect, is probably quite sound.

That a monohybrid heterosis exists also when non-lethal mutations are considered (cf. RASMUSSON, p. 264 above, and the genes *T*, *K* and *G* in *Apotettix*, p. 269), is shown by a paper of TIMOFÉEFF-RESSOVSKY (1940, his Fig. 7). The gene *A* in *Drosophila funebris* causes increased viability in heterozygous state compared with both homozygotes *AA* and *aa* (an approximate difference of 10 % and 30 % respectively). Unfortunately, the number of individuals is not given. Since the same figure is reproduced by BAUER and TIMOFÉEFF-RESSOVSKY (1943, in their Fig. 11), the difference is probably significant from a statistical point of view. In

some experiments the gene *ebony* in *D. melanogaster* shows a similar effect (l. c., p. 402, Fig. 70; cf. MASING's results).

SOME FURTHER CASES OF MONOHYBRID HETEROSIS IN BARLEY.

As pointed out previously, the fully conclusive experiment is to obtain a spontaneous mutation that has arisen in a pure line, and then to compare its heterozygote with normal sister-plants from the same segregating progeny.

For the barley breeding of North Europe the old strain »Golden Barley» has played an important rôle. It was isolated in 1897 from an old peasant variety (Gotland), brought into the market about fifteen years later and first fully substituted by other varieties in the beginning of the thirties.

From this pure line NILSSON-EHLE obtained a series of spontaneous mutants. Two such mutants are denoted as *xantha* 3 and *albina* 7. The latter is no real *albina*, but a »*virido-albina*» type (GUSTAFSSON, 1940), which turns white at low temperatures. These two spontaneous mutations have been combined and the dihybrid segregates according to 9 : 3 : 4. No synthetic lethality (cf. GUSTAFSSON, 1938) of any kind is present. The germination of dihybrid, monohybrid and normal seeds is complete in *fresh material*, and the fertility is in no way decreased. In one special analysis the number of sterile flowers amounted to 2,9 % in the dihybrids, to somewhat less in monohybrids, and to 2,5 % in normally homozygous plants.

Both mutants have lethal character. The recessive seedlings die at an age of two or three weeks, when the nutriment of the seed is consumed. Owing to defects in the chlorophyll apparatus no assimilation is possible. In addition, however, recessive seeds show a type of true (not indirect) lethality. They lose their capacity of germination much faster than the heterozygous and dominant homozygous seeds. This is especially striking in the case of *xantha* 3. Seeds homozygous for the mutation cannot germinate at all after a storage of three years. After two years the decrease in germination is noticeable.

INCREASE IN VIGOUR.

The material available does not suffice for *definite* conclusions regarding the general vigour of heterozygotes. The present writer has made no special effort to gather the large material necessary. Mono-

hybrid heterozygotes of both mutations are superior to their normal sister-plants in various respects, likewise the dihybrids. Different materials give somewhat different results. The heterozygotes always excelled the normal homozygotes in one or more properties. Frequently they were generally superior. The material analysed in 1945 gave uniform results regarding the superiority of *xantha* 3 and *albina* 7 heterozygotes.

THE PECULIAR SEGREGATION OF XANTHA 3.

It was mentioned on p. 267 that F_1 plants heterozygous for *xantha* 3 gave an excess of recessives in the F_2 when they were weak (possessed a low number of ears), but gave a deficiency when they were well-developed and contained a great number of ears. The difference between the two groups was statistically significant ($0{,}01 > P > 0{,}001$).

TABLE 2. *The segregation of xantha 3 heterozygotes.* (Fresh material.)

No. of heads per plant	Calculated No. of seeds per head	No. of progenies	Segregation	% recessives
2	19,9	12	336 — 141 = 477	29,6
3	19,4	9	384 — 141 = 525	26,9
4	19,8	19	1132 — 376 = 1508	24,9
5	19,6	10	722 — 259 = 981	26,4
6	21,8	4	404 — 120 = 524	22,9
7	21,2	3	349 — 97 = 446	21,7
8	22,4	1	145 — 34 = 179	19,0
9	22,3	4	634 — 170 = 804	21,1
11	22,1	2	372 — 114 = 486	23,5
2—5	19,7	50	2574 — 917 = 3491	26,3
6—11	22,0	14	1904 — 535 = 2439	21,9
Total material	20,6	64	4478 — 1452 = 5930	24,5

After 1938 a great number of progenies were analysed. They gave the following results (Table 2). All data refer to fresh material.

The plants producing few ears also show a low kernel number. Thus they are weak in two respects. The segregation data of weak plants, compared with those of strong plants, give such a high χ^2 value that P is much less than 0,001 (2 × 2-table, 1 D. F.). If the χ^2 is calculated for all nine classes (9 × 2-table, 8 D. F.) its value will be 20,91 with $0{,}01 > P > 0{,}001$, i. e. also here a high significance.

The material is derived from two different years. Similar results

were also obtained in an analysis of the year 1945. Thirty kernels from a great number of heterozygotes and homozygotes were put for germination. In one offspring a segregation of 12 green : 13 *xanthas* was recorded (P less than 0,01). This plant contained three ears and consequently belonged to the weak plants. No similar aberration appeared in the strong sister-plants.

The total material gives a segregation ratio of 4478 : 1452 = 5930, with $0{,}5 > P > 0{,}3$, i. e. in fair agreement with the 3 : 1 proportion. This agreement is only apparent, it covers great fluctuations in segregation.

The cause of this deviation must be related to changes in the gametic behaviour. No zygotic lethality whatsoever is present, whether in early embryo development or in germination.

Three possibilities exist: (1) In weak plants gametes carrying the mutation are formed in excess, to more than 50 %. In strong plants, on the other hand, a deficiency of such gametes arises. (2) Selective fertilization is present; recessive eggs of weak plants prefer sperms of their own kind. (3) Pollen grains carrying the mutation are favoured in weak plants owing to more rapid germination or growth of their tubes.

A change in the *number* of recessive pollen grains would require some special disturbance of meiosis. This is difficult to conceive, for no trace of any sterility is present.

In many instances a selective fertilization may seem to meet the truth. In a plant heterozygous for *xantha* 3 a new *xantha* mutation was produced by irradiation, and the dihybrid segregated nicely according to 9 : 3 : 3, instead of 9 : 3 : 4. Double-recessives did not appear. Probably they were not even formed. No obvious sterility was present. This explanation is hardly possible, however, in the *xantha* 3 case itself.

The disturbed segregation ratios therefore probably depend on some physiological response of the pollen grains to the properties of the mother plants, i. e. the possibility denoted above as No. 3.

Whatever the right explanation, processes must occur which in a certain internal environment favour the recessive factor, in another environment favour the dominant. Weak plants result in general after a strong competition in seedling stage. This prevents rich tillering and rich seed formation. Consequently, *xantha* 3 gametes profit when competition gets harder.

DURATION OF LIFE.

The segregation of *albina* 7 is in all respects normal. According to GUSTAFSSON (1938, p. 46), it was at that time 807 : 289 = 1096 with

P = 0,3. More material has been gathered since then. In all, the segregation of fresh material has been 3810 : 1259 = 5069, P = 0,8. There is a small deficit of recessives, their frequency being 24,8 %. The recessive seedlings decrease their sprouting ability, which was indicated by special experiments in the thirties.

In the fall of 1945 an extensive material, originating from the harvested pedigrees of 1943 and 1942, was put to germination in the

TABLE 3. *Germination and segregation of albina 7 and xantha 3 heterozygotes.*

	Germination	Segregation	P	No. of progenies
A 7 heterozygotes 1943	98,1 %	810 : 251 = 1061	0,3	36
Normal sister-plants 1943 ...	98,0 %			18
A 7 heterozygotes 1942	64,2 %	698 : 149 = 847	< 0,001	44
Normal sister-plants 1942.....	58,6 %			21
X 3 heterozygotes 1943	85,3 %	1359 : 330 = 1689	< 0,001	66
Normal sister-plants 1943.....	93,2 %			37
Dihybrid plants 1943	76,0 %	351 : 89 : 153 = 593	0,1 > P > 0,05	26
X 3 heterozygotes.....	73,8 %	272 : 60 = 332	0,01 > P > 0,001	15
A 7 heterozygotes.....	74,2 %	135 : 43 = 178	0,8	8
Normal sister-plants	70,7 %			5

(30 kernels sown of each progeny.)

laboratory. The number of ears, seeds per plant and seed weight were previously recorded for *albina* 7 and *xantha* 3 monohybrids, as well as for their dihybrids, and for normal plants. Thirty seeds of each plant were sown. Soil, temperature and moisture were the best possible.

It was immediately found that heterozygotes of *xantha* 3 gave a great deficit of recessives. This was the case already in the 1943 cultures but was especially evident in the 1942 material. Here almost no *xanthas* appeared, either in mono- or in di-hybrids. Apparently most recessive *xantha* seeds lose their capacity to germinate in a very short time.

Similar, though not so pronounced, was the case with *albina* 7. In 1943 the segregation was quite regular and the total germination of the heterozygotes normal. In 1942 it was highly decreased (Table 3).

TABLE 4. *Segregation in its relation to germination.*
(Albina 7 heterozygotes, 1942.)

	Germination 0 — 50	50 — 67	67 — 90	90 — 100 %	No. of progenies
I					
Segregation	80—12= 92	317—56=373	237—63=300	64—18=82	44
P.....	$0{,}01 > P > 0{,}001$	$< 0{,}001$	0,1	$0{,}7 > P > 0{,}5$	(30 kernels
% recessives	13,0	15,0	21,0	22,0	of each)
II					
Segregation	398—68=466	236—64=300	86—23=109	—	8
P.....	$< 0{,}001$	$0{,}2 > P > 0{,}1$	$0{,}5 > P > 0{,}3$	—	(All seeds
% recessives	14,6	21,3	21,1	—	sown)

TABLE 5. *Segregation in its relation to germination.*
(Xantha 3 monohybrids and dihybrid material.)

	Germination 0 — 90	90 — 100 %	No. of progenies
Xantha 3 1943			
Segregation.....	740 : 157 = 897	619 : 173 = 792	66
P.....	$< 0{,}001$	$0{,}05 > P > 0{,}02$	
% recessives	17,5	21,8	
Dihybrid material 1943			
Dihybrid plants	279 : 65 : 108 = 452	72 : 24 : 45 = 141	26
P.....	0,02	$0{,}2 > P > 0{,}1$	
% recessives	38,3	48,9	
X 3 heterozygotes.....	206 : 45 = 251	66 : 15 = 81	15
P.....	0,01	$0{,}2 > P > 0{,}1$	
% recessives	17,9	18,5	
A 7 heterozygotes	98 : 25 = 123	37 : 18 = 55	8
P.....	$0{,}3 > P > 0{,}2$	$0{,}2 > P > 0{,}1$	
% recessives	20,3	32,7	

(30 kernels sown of each progeny.)

The dihybrid and the *xantha* 3 monohybrid materials of 1942 cannot be satisfactorily analysed, since only a few *xantha* recessives appeared. Therefore many series denoted as green homozygotes were in fact heterozygous. That the dihybrid material of 1943 did not germinate normally, depends probably rather on differences in storage

(high water content, etc.) than on differences in genotypic structure. The normal sister-plants of the dihybrid material were likewise inferior in germination.

It can be definitely stated that the disturbed segregation ratios occurring are directly caused by the poor germination of recessive seeds. This is shown by the following surveys (Tables 4 and 5), illustrating the course of segregation when germination is almost normal (27—30 seeds germinated) and when it is markedly decreased.

There seems to be no doubt that recessive seeds are the first to age and die. Some are incapable of germination in the subnormal group as well (27—30 germinated seeds), especially when *xantha* recessives are concerned. In *albina* 7 three progenies with 27, 27 and 28 germinated seeds gave 19, 23 and 25 % recessives respectively (22 : 5, 21 : 6, 21 : 7).

The lower part of Table 4 is made up of segregation data for eight heterozygous plants, selected after the first analysis, with 150 kernels per plant or more.

In those cases where germination is manifestly affected (dihybrid material 1943, *albina* 7 material 1942) the seeds of heterozygous plants germinated better than seeds of normal homozygotes *from the same offspring*. This is the more striking because recessive seeds form about one quarter of the seeds of the heterozygotes and lose their capacity to germinate very rapidly. The dihybrid plants also show better germination than both monohybrids and these in their turn better than the normal plants.

An analysis of the *albina* 7 material from 1942 *proves* in fact that the heterozygous seeds keep their viability better than both homozygotes.

In all, 1320 seeds from heterozygous *albina* 7 plants were sown. In the case of an exact 3 : 1 proportion they would consist of 990 dominant and 330 recessive seeds. The standard error amounts to 15,73. For a correct interpretation of the data, instead of working with this proportion, we must calculate with a segregation in which the recessives are diminished by three times the standard error (47,19 individuals) and the dominant seeds increased by the same number. In such a case we obtain $1037{,}19 : 282{,}81 = 1320$.

The actual segregation was $698 : 149 = 847$. This gives a minimum germination of $67{,}30 \pm 1{,}46$ % for the sum of heterozygous and normal homozygous seeds, and a maximum germination of $52{,}69 \pm 2{,}97$ % for the recessive seeds. The germination of the normal homozygotes was $58{,}57 \pm 1{,}96$ %. Thus, even if we assume such a high deviation from the normal 3 : 1 ratio as three times the standard error, we find a much

lower germination of the normal homozygous seeds than of the sum of heterozygous and normal homozygous seeds. The difference amounts to $8{,}73 \pm 2{,}44$ % with a P value less than 0,001. As a matter of fact the *total* progeny of the heterozygotes germinated to 64,17 %. This alone implies a difference of $5{,}60 \pm 2{,}37$ %, with $P = 0{,}02$.

TABLE 6. *Germination of seeds from heterozygous and normal sister-plants.*

	Kernel production per plant				
	0 — 50	50 — 100	100 — 150	150 — 200	200 — 400
Heterozygotes					
Number of seeds sown	150	510	360	120	150
Segregation...	54 — 10 = 64	274 — 51 = 325	206 — 51 = 257	67 — 15 = 82	82 — 18 = 100
Total germination	42,67 %	63,73 %	71,39 %	68,33 %	66,67 %
Calcul. germin. of dominant and heteroz. seeds after 3 : 1	48,00 %	71,63 %	76,30 %	74,44 %	72,89 %
Homozygotes					
Number of seeds sown	60	330	150	60	30
Germination	65,00 %	60,91 %	55,33 %	43,33 %	66,67 %
Difference between hetero- and homozygotes...	$-22{,}33 \pm 7{,}36$ %	$2{,}82 \pm 3{,}43$ %	$16{,}06 \pm 4{,}71$ %	$25{,}00 \pm 7{,}68$ %	—
P.....	$0{,}01 > P > 0{,}001$	0,4	$< 0{,}001$	0,001	—

The same material can be treated in another way. It was found when examining the segregation of *xantha* 3 that the vigour of the heterozygote determined the mode of segregation. A similar classification can also be used for the *albina* material. Here we know the exact number of seeds produced by every plant, either heterozygous or homozygous. Weak plants are characterized by a low number of ears and kernels, as well as by small light seeds.

Therefore we may divide the 43 heterozygotes into five groups (Table 6; one plant must be omitted).

Very weak plants with fewer than fifty seeds give a significantly higher germination of green homozygotes than of heterozygotes (comprising the entire seedling material). The calculated germination of normal and heterozygous seeds, with *albinas* disregarded, is still inferior.

Rather weak plants with 50—100 seeds give a high germination in the case of heterozygotes, a low in the case of homozygotes. The difference is not significant. The calculated germination of normal and heterozygous seeds is very high.

Rather strong heterozygotes with 100—150 seeds show a superior *total* germination ($P < 0{,}001$).

The same is evidently true of the strong plants with 150—200 seeds. In spite of the high standard errors the difference becomes significant ($P = 0{,}001$).

In the strongest plants with 200—400 seeds no significant difference is found. The calculated germination for the sum of normal and heterozygous seeds is very high.

This analysis proves, I think, that seeds heterozygous for the chlorophyll defect *albina* 7 keep their average life longer than homozygous seeds of both kinds. This is especially obvious in medium strong and strong plants. The behaviour of weak plants illustrates another feature characteristic of lethals in single dose: the great range of modification, the high plasticity.

PLASTICITY.

Repeatedly it has been found, after analysing segregating progenies, that heterozygotes form a high number of ears more readily than normal homozygotes. Nevertheless, the average ear number is approximately the same in both instances. This must depend on the fact that the heterozygotes also readily produce very few ears. They ought to display a greater power of modification, a higher variability.

Eighty *albina* 7 heterozygotes gave an average ear number of 4,92 with $\sigma = 2{,}54$ and v_1 (the variation coefficient) $= 51{,}62$. Similarly 39 homozygotes produced 4,67 ears per plant, σ equalling 1,77 and v_2 37,90. The proportion of v_1 to v_2 is 1,36.

Sixty-six *xantha* 3 heterozygotes showed an average number of 4,23 ears, $\sigma = 1{,}50$, $v_1 = 35{,}46$. The corresponding figures of 37 normal sister-plants were 4,08, $\sigma = 1{,}23$, $v_2 = 30{,}14$. The proportion amounts to 1,18.

Calculated in the same manner for kernel number and kernel weight the indices in *albina* 7 are 1,32 and 1,30, in *xantha* 3 1,16 and 1,06. The mean of all six values is 1,23.

The figures of *albina* 7 refer to the total number of plants in 1943 and 1942. Both years behave in a similar way. The examples could be multiplied. In this discussion I prefer to turn to the material already

TABLE 7. *The proportion of variation coefficients in heterozygous and homozygous material.* (Calculated after ROBERTSON, 1932, and ROBERTSON and AUSTIN, 1935.)

Mutation	Origin	v_1/v_2					Average	No. of comparisons
		Number of grains per plant	Grain weight per plant	Number of heads per plant	Length of culm	Length of head		
Monohybrids								
Xantha	Black Hulless	1,03	1,02	1,04	1,05	1,06	1,04	3
Albina$_c$	Colsess	1,00	0,95	1,30	1,00	1,06	1,06	2
Albina$_{c_3}$	»	1,05	1,01	1,03	1,02	1,03	1,03	2
Albina$_c$	Canada Thorpe	1,15	1,01	0,94	1,07	1,87	1,21	2
Xantha$_c$	Colsess	0,99	1,08	1,08	0,88	1,03	1,01	1
Albina	Hanna	1,02	1,13	1,33	0,98	1,02	1,10	1
Dihybrids								
$A_c + X_c$	Colsess	1,00	1,01	0,98	1,03	1,02	1,01	1
$A_{c_3} + X_c$	»	1,19	1,04	0,97	0,99	1,23	1,08	1
Average		1,05	1,03	1,08	1,00	1,17	1,07	

v_1 = variation coefficient of heterozygote
v_2 = » » » homozygote

published by ROBERTSON and his collaborator (1932, 1935) and comprising no fewer than 6000 plants. They give the standard errors (m) for every set of measurements. From their data σ can be computed by multiplying by $\sqrt{n}$ (n = the number of individuals).

$$v = \frac{100 \cdot \sigma}{M} = \frac{100 \cdot m \cdot \sqrt{n}}{M}$$ (JOHANNSEN, 1926, p. 58).

The authors measured length of head, number of culms, length of culm, and, in addition, the extremely important properties of kernel number and kernel weight per plant. When more than one series of measurements was performed (Table 7, column 9), the mean is given. We obtain the above indices.

Almost always the variability of the heterozygotes surpasses that of the homozygotes. In fourteen cases out of 40 the index is higher than 1,05, as against two cases with the index below 0,95. The mean of all indices is $1{,}067 \pm 0{,}025$. The difference from 1,000 gives a t-value of 2,69 with $P = 0{,}01$. (The dihybrids give $M = 1{,}046$; two lethals brought together are consequently not so effective.) Excluding the dihybrid cases, we obtain the even higher mean of 1,074, but the t-value is lower owing to the smaller number of cases. Nevertheless the difference is rather great, $t = 2{,}32$, $P = 0{,}03$.

The four mutations on the top of the table, for which repeated sets of measurements have been performed, give the still higher index of 1,085.

All six lethals show an enhancing effect, three of them increase plasticity by more than 5 %. We may therefore conclude that the variability is substantially greater in plants having one lethal in heterozygous state than in plants of a pure line.

As seen in the table, the length of ears reacts readily; next to that the number of ears per plant. Least affected is the length of the culm. Here we find two cases having a rather high variability of the heterozygote, and one with very low. The heterozygote of the very poor mutation, originated in Canada Thorpe and damaging endosperm (as well as embryo), responds to the internal poisonous condition by an extremely high variability (the mean = 1,21), not only in length of ear but also in kernel number and culm length. It is however poor in tillering. *Albina*$_c$ from Colsess is also characterized by a high variability, similarly the *albina* type from the old Moravian line Hanna. *Xantha*$_c$ from Colsess shows an increased index in grain weight and number of ears, a highly decreased one in length of culm, hence producing a normal average.

The dihybrid made up of *albina*$_c$ and *xantha*$_c$ has a normal variability, possibly decreased in number of heads. The dihybrid, consisting of *albina*$_{c3}$ and *xantha*$_c$, has a high average. This is of interest since it indicates a special interaction of different lethals, a_{c3} shows by itself an almost normal variability, but together with x_c it reacts more strongly than a_c that has a higher index.

The fundamental results of this discussion are that properties like length of ear, number of culms, weight of seeds are made more variable by mutations that work on the chlorophyll formation and destroy it in homozygous state. These properties are not influenced by the mutations themselves but by their heterozygous condition. The latter functions in the same way as polygenes are said to do, according to MATHER. It

seems to me that this fact also throws some further light on the polygenic question.

The author is fully aware that exceptions, and most important ones, may be raised in repudiation of these results. In addition, the v_1/v_2 indices given above rest upon indirect calculations. *If* these are substantially valid — and they are amply confirmed in the author's own material — a principle of far-reaching consequences has been revealed in ROBERTSON's and his co-worker's papers.

In this connection it is well worth mentioning that a similar treatment of KARPER's and MANGELSDORF's data gives average indices of 1,00 and 0,96 respectively. The heterozygous variability as to head length is considerable in *Sorghum*, almost normal in maize. Very peculiar is the pronounced variation in height of young heterozygotes in comparison with the mature plants. The v_1/v_2 indices of this property change successively from 1,27 to 0,73 in *Sorghum* and from 1,09 to 0,89 in maize. It appears as if the heterozygous variability, so striking in young stages, would gradually narrow down. (Compare the relatively low v_1/v_2 indices of culm length in barley.)

CONCLUSIONS AND DISCUSSION.

The facts reported above may be summed up as follows:

Dating back to KARPER, 1930, or possibly RASMUSSON, 1927, a series of investigations have shown that mutations, many of which are lethal in homozygous condition, increase vigour when they occur in single dose. The first definite data were gathered by ROBERTSON (1932).

Vigour can be increased also in the most general sense, with respect to the vegetative as well as the reproductive phase. Such is the effect of several chlorophyll mutations which influence culm length, ear length, number of culms, but also number of flowers, kernel production and kernel weight.

Duration of life or — to speak more precisely — the preservation of seed germination is improved in certain cases.

The increased vigour in animals has not been proved for more than part of the life cycle. Competitive ability of juvenile stages is strengthened in *Apotettix* and *Drosophila*.

One *xantha* mutation, lethal when homozygous, favours the gametes possessing it under certain internal conditions. Such is the case when the heterozygous plants are weak.

The heterozygous lethal condition enhances plasticity. It works on properties in no way related to the homozygous effect of the lethal.

It appears from the previous survey as if lethal mutations in single dose would be more effective in pure lines of cereals than in cross-breeding populations of *Drosophila*. Of the reported chlorophyll cases many increase vigour, but only a few lethals in *Drosophila* do so. It is now a well-known fact that lethals are rather frequent in cross-breeding populations of plants and animals (in the second chromosome of *Drosophila melanogaster* from the Crimea population to no less than 22 %; MASING). The populations are stuffed with lethals in heterozygous condition. These arise frequently. In order to survive they must be forced into a very complex equilibrium system. Taken out of this harmonious entirety and brought into laboratory stocks, many produce no effect or even a destructive heterozygous one (as indicated by MASING's work). In pure lines of cereals their result seems to be more readily produced and also more conspicuous.

The interaction of heterozygous lethals with other chromosome parts has been specially examined by MASING. These experiments involved second chromosome lethals on the one hand and the third chromosome factor *ebony* on the other, but also crossing over products of the second chromosome itself. A further instance is provided by ROBERTSON's data. The factors x_c and a_{c3} induce a higher variability of the dihybrid than the factors x_c and a_c, although a_c itself works stronger than a_{c3}.

The importance of monohybrid heterosis for the conception of inbreeding has already been discussed by STUBBE and PIRSCHLE. The reader is referred to their paper. It is immediately evident that the original hypothesis of SHULL (1911) must form one foundation-stone of all theories regarding inbreeding degeneration. Of course, it does not exclude the linkage explanation. Seen in the light of the presented data, the poor segregates obtained after inbreeding are not a cause of inbreeding degeneration. They are the unfortunate consequences of the homozygotization and the break-down of the harmonious whole, where lethals play an important and frequently a positive rôle.

Of even higher importance is the monohybrid heterosis for evolutionary problems. A mutation may show divers effects on viability in single and in double dose. Consequently, we cannot discuss its evolutionary significance until we know how it works both as homozygote and as heterozygote. Furthermore, it may spread in gametic

status, also when its homozygote is »monster-like». Successively, modifiers and position effects will work also on its homozygous appearance. To take one extreme example. *Albina*, *xantha* or *viridis* mutations, destroying the chlorophyll apparatus, will remain lethal when homozygous, until the individual, carrying one such factor, has changed to a parasite or saprophyte by means of other mutations. A very rare phenomenon, it is true, but nevertheless happening once in a while.

Since DARWIN's time it has been discussed over and over again why animals and plants try to keep or improve their cross-fertilizing ability. There must be some properties connected with heterozygosity that contribute to this state of things. *One* such property is indicated by this survey: the higher plasticity, the greater range of modification. We know that dominance, viz. recessivity, are relative phenomena (see, for instance, TIMOFÉEFF-RESSOVSKY, 1940). In a certain sense a heterozygote may be said to cover the range of variability from the dominant to the recessive pattern. Lethals in single dose work in much the same way. In addition, they increase modification in properties entirely foreign to their own specific action. Consequently, the heterozygous condition is a pre-requisite for high modificative ability. The single lethal makes the constitution more labile. The plasticity of the individual is increased. The pure line is fundamentally a draw-back in evolution.

No full explanation of this heterosis effect of lethals can be given. One parallel can be drawn, however. We know that certain substances (growth hormones and other hormones, metallic salts, etc.) stimulate development in very small concentrations but act as poisons when their amount is too high. Similarly, the total amount of the »substance» produced by two identical lethals may destroy the normal course of development, the amount produced by one such lethal will aid by oiling the machinery. This metaphore is of course rather crude. Since the interaction of lethals with other genes or chromosomes is proved, the idea is also close at hand that the lethal may prevent some inhibitive substance from action and so indirectly augment the effect of another.

SUMMARY.

Series of data are presented which go to show that mutations lethal in homozygous condition may increase viability when they occur in the single dose.

Vigour may also be affected in a general sense: In some plants the reproductive capacity is increased along with properties such as length of culm, length of head and ability of tillering.

Heterozygous seeds of the mutation *albina* 7 keep their germination capacity longer than the homozygous seeds of both kinds. This is especially conspicuous in medium strong and strong plants.

A tendency exists to increase the range of variation in mono- and di-hybrids in comparison with the homozygous sister plants.

Some general problems on population dynamics and inbreeding degeneration are briefly discussed.

The author is indebted to Dr. O. TEDIN, Svalöf, for discussions on statistical matters.

For further data see also a paper by GRANHALL in this issue of Hereditas.

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CONTENTS.

Introduction 263
Previous results in plants 264
Previous results in animals 268
Some further cases of monohybrid heterosis in barley 272
Increase in vigour 272
The peculiar segregation of *xantha* 3 273
Duration of life 274
Plasticity 279
Conclusions and discussion 282
Summary 284
Literature cited 285

ON HETEROSIS EFFECTS IN TRITICUM VULGARE

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IN many cross-fertilizers hybrid vigour is a well-known phenomenon, appearing especially in crosses between more or less inbred strains. Interspecific crosses are also often characterized by luxurious hybrid plants. In the self-fertilizing genus *Triticum* the latter case can be exemplified by the pentaploid cross *vulgare* × *durum*, where the F_1 plants are taller and have more culms than the parents (GRANHALL, 1943, p. 288). In self-fertilizing plants hybrid vigour is otherwise described only comparatively few times. Thus, MÜNTZING (1945) records data from seven different species, and GUSTAFSSON (1946) has gathered some interesting examples of improved viability in heterozygotes from chlorophyll mutants and other lethals. Among MÜNTZING's references *Triticum vulgare* is also represented (ENGLEDOW and PAL, 1934).

THE CROSS HINDI × EXTRA-KOLBEN II.

In 1933 I received from Professor ÅKERMAN an F_2 material of the cross Hindi × Extra-Kolben II, growing in the field at Svalöf. Both parents belong to the spring form of *T. vulgare*. Hindi is an Egyptian variety with a very short straw, bearded heads and white grains. Extra-Kolben II is selected from Extra-Kolben I, derived from a cross between two Svalöf lines out of German varieties (Kolben × 0201, Emma). It is tall, beardless and red-grained. Hindi and Extra-Kolben II also differ in several other morphological and physiological characters.

Taken all together the F_2 comprised 6499 plants, 93 of which, however, did not shoot but remained in the tussock stage. These plants evidently represented triple-recessives of the spring-form factor. The actual segregation (6406: 93) is in good agreement with a 63 : 1 expectation ($6397{,}_{45} : 101{,}_{55}$; $\chi^2 = 0{,}_{731}{}^{000}$, $0{,}_{50} > P > 0{,}_{30}$; as to the indices of χ^2 and t, see GRANHALL, 1943, p. 278). Cases of trimeric segregation of the spring factor I have found previously reported only twice: by

POWERS (1934) and by ÅKERMAN (1943). POWERS explained the segregation in the cross Velvet Node (spring form) × Hybrid 128 (winter form) by assuming three factors, two of which were dominant for spring form, and the third one for winter form. In the cross Master (spring form) × Kron (winter form), analysed by ÅKERMAN, the three factors were all dominant for spring form. The case Extra-Kolben II × Hindi seems to be the first described one in which two spring wheats have given rise to winter segregates. According to ÅKERMAN Extra-Kolben II is monofactorial, and the segregation can thus be explained by the assumption that Hindi has two other spring-wheat factors. From a theoretical point of view the hypotethical formulae $S_K S_K S_S S_S S_M S_M$ for Master (cf. ÅKERMAN, l. c.) and $S_K S_K S_S S_S S_H S_H$ for Hindi should be tested in order to manifest the identity or non-identity of S_M and S_H. Master and Hindi seem to belong to geographically and morphologically very distant forms, and they consequently offer a very good chance of testing the existence of trimery or tetramery as to the dominant spring-wheat factor. It must, however, be mentioned that the possibility of some common ancestry for the two varieties is not quite excluded (*ex* India?). The existence of dominant winter factors accepted by POWERS and several other American investigators also needs a thorough test.

As to grain colour, monofactorial segregation was found. Only 267 plants were examined for this character, 201 having red and 66 white grains (expected $200{,}25 : 66{,}75$; $\chi^2 = 0{,}011^{000}$, $0{,}90 > P > 0{,}80$).

The specific purpose in studying this cross, however, was to find out whether there was any real correlation between beardness and plant development. When selectioning F_2's of crosses between bearded and beardless varieties, Professor ÅKERMAN had several times observed that an unproportionally great number of the most vigorous plants belonged to the bearded or half-bearded categories. The F_2 of Hindi × Extra-Kolben II was thus assorted into beardless, heterozygous and bearded plants. Plant height, number of culms and weight of grains were recorded. The investigation comprised 660 beardless, 1248 heterozygotes and 595 bearded plants. Expected figures were $625{,}75 : 1251{,}50 : 625{,}75$; $\chi^2 = 3{,}396^{00}$, $0{,}20 > P > 0{,}10$. The segregation can thus be considered normal in spite of the tendency to surplus of beardless and lack of bearded plants.

The data are gathered in Table 1. The parents showed a marked difference in plant height, Extra-Kolben II being about 50 % taller. Hindi, on the other hand, showed a higher tillering capacity than

TABLE 1. *Data of vigour in Hindi × Extra-Kolben II.*

	Number of plants	Height of straw, cm	Culms per plant	Grain weight per plant, gms
Parents:				
Extra-Kolben II	63	$106{,}8 \pm 1{,}08$	$2{,}97 \pm 0{,}157$	—
Hindi	50	$69{,}5 \pm 1{,}43$	$3{,}44 \pm 0{,}316$	—
F_2 plants:				
Beardless	660	$98{,}9 \pm 0{,}40$	$2{,}53 \pm 0{,}045$	$1{,}70 \pm 0{,}097$
Heterozygotes	1248	$99{,}0 \pm 0{,}29$	$2{,}71 \pm 0{,}037$	$2{,}07 \pm 0{,}076$
Bearded	595	$97{,}1 \pm 0{,}43$	$2{,}58 \pm 0{,}048$	$1{,}86 \pm 0{,}114$
Differences:				
Hindi—Extra Kolben II				
Diff.	—	$-37{,}3 \pm 1{,}79$	$0{,}47 \pm 0{,}352$	—
t	—	$20{,}84^{***}$	$1{,}34^{00}$	—
Heteroz.—Beardless				
Diff.	—	$0{,}1 \pm 0{,}49$	$0{,}18 \pm 0{,}058$	$0{,}37 \pm 0{,}123$
t	—	$0{,}20^{000}$	$3{,}10^{**}$	$3{,}01^{**}$
Heteroz.—Bearded				
Diff.	—	$1{,}9 \pm 0{,}52$	$0{,}13 \pm 0{,}061$	$0{,}21 \pm 0{,}137$
t	—	$3{,}65^{***}$	$2{,}13^{*}$	$1{,}53^{00}$
Bearded—Beardless				
Diff.	—	$-1{,}8 \pm 0{,}59$	$0{,}05 \pm 0{,}066$	$0{,}16 \pm 0{,}150$
t	—	$3{,}05^{**}$	$0{,}76^{000}$	$1{,}07^{000}$

Extra-Kolben II, but this difference is not sufficiently significant. The grain weights of the parental plants were not recorded.

The F_2 plants showed a surprisingly narrow variation in plant height, as seen by the standard errors. The bearded plants were on an average shorter than the half-bearded and beardless ones, and these differences — though small — were clearly significant. The heterozygotes were insignificantly taller than the beardless plants. As compared with the parents, F_2 did not quite reach the tallest one, Extra-Kolben II.

In culm number, which is a very good characteristic of the general vigour, the half-bearded heterozygotes were significantly richer than the homozygous groups. These last-mentioned groups, besides, showed the same tendency of difference as did the parental varieties, the bearded ones being somewhat better tillered. It was also made clear that the half-bearded and bearded groups really contained a greater number of especially vigorous plants than the beardless group, the

percentage of plants with at least five culms being 3,6 in the beardless, 9,2 in the half-bearded and 5,7 in the bearded group.

In grain weight the same order was found, the heterozygotes giving the highest value, the beardless homozygotes the lowest one. Only the difference heterozygote — beardless was however significant.

The investigation had consequently given a result agreeing with the breeder's suspicion in so far as the bearded plants of the cross had on an average proved superior to the beardless ones. The most striking finding was, however, the distinct advantage of the heterozygotes. A pleiotropic effect of the beardness factor or some absolute linkage between beardness and one or several quantitative factors could not thus alone give a satisfactory explanation of the results obtained. There were also reasons to suspect some kind of heterosis effect.

THE CROSS PANSAR × BEARDED PANSAR.

In order to study the problem closer the winter-wheat cross Pansar × Pansar b was carried out in 1934. The parents were received from Professor NILSSON-EHLE's material at the Institute of Genetics. They only differed in one single factor, Pansar b being a spontaneous beardness mutation discovered in Pansar. The cross is briefly mentioned in another connection in a previous paper (GRANHALL, 1943, p. 284, cross No. 15). F_2 was analysed in about the same manner as described above. Straw height, number of culms, grain weight and also number of grains were recorded. Plots of the parental varieties sown for comparison were also analysed. The results are compiled in Table 2.

The bearded mutant parent is a little shorter than Pansar itself but is somewhat superior in the other respects. The differences were, however, quite small, and only one of them proved significant. This exception referred to the number of culms, which was remarkably higher in the mutant than in the original Pansar.

The assorting of the segregation was not so easy as in the Hindi × Extra-Kolben II cross. Most dubious plants were, however, controlled in the F_3, and correction was thus possible. The segregation was 480 beardless : 776 heterozygous : 368 bearded plants. This does not answer very well to the expectation (405 : 810 : 405; $\chi^2 = 17{,}693^{***}$, $P < 0{,}001$). There is a very marked over-representation of the beardless group, which may — at least partly — depend upon mistakes in the assorting. The F_3 control has, however, not given any reasons to suspect that the mistakes have influenced the averages of the data found. The deficit

TABLE 2. *Data of vigour in Pansar × Pansar b.*

	Number of plants	Height of straw, cm	Culms per plant	Grain weight per plant, gms	Number of grains per plant
Parents:					
Pansar	326	$93{,}5 \pm 0{,}72$	$2{,}55 \pm 0{,}088$	$3{,}67 \pm 0{,}150$	$96{,}0 \pm 3{,}76$
Pansar b	404	$92{,}7 \pm 0{,}50$	$2{,}65 \pm 0{,}076$	$4{,}29 \pm 0{,}138$	$102{,}3 \pm 3{,}23$
F_2 plants:					
Beardless	480	$92{,}2 \pm 0{,}59$	$2{,}40 \pm 0{,}074$	$3{,}50 \pm 0{,}130$	$85{,}9 \pm 2{,}89$
Heterozygotes	776	$94{,}3 \pm 0{,}32$	$2{,}62 \pm 0{,}058$	$4{,}08 \pm 0{,}094$	$98{,}8 \pm 2{,}34$
Bearded	368	$89{,}1 \pm 0{,}69$	$2{,}41 \pm 0{,}078$	$3{,}90 \pm 0{,}155$	$91{,}6 \pm 3{,}51$
Differences:					
Pansar b—Pansar					
Diff.	—	$-0{,}8 \pm 0{,}88$	$0{,}10 \pm 0{,}116$	$0{,}62 \pm 0{,}204$	$6{,}3 \pm 4{,}96$
t	—	$0{,}91^{000}$	$0{,}86^{000}$	$3{,}04^{**}$	$1{,}27^{000}$
Heteroz.—Beardless					
Diff.	—	$2{,}1 \pm 0{,}67$	$0{,}22 \pm 0{,}094$	$0{,}58 \pm 0{,}161$	$12{,}9 \pm 3{,}72$
t	—	$3{,}14^{**}$	$2{,}35^{*}$	$3{,}60^{***}$	$3{,}47^{***}$
Heteroz.—Bearded					
Diff.	—	$5{,}2 \pm 0{,}76$	$0{,}21 \pm 0{,}097$	$0{,}18 \pm 0{,}182$	$7{,}2 \pm 4{,}22$
t	—	$6{,}84^{***}$	$2{,}16^{*}$	$0{,}99^{000}$	$1{,}71^{0}$
Bearded—Beardless					
Diff.	—	$-3{,}1 \pm 0{,}90$	$0{,}01 \pm 0{,}107$	$0{,}40 \pm 0{,}202$	$5{,}7 \pm 4{,}55$
t	—	$3{,}44^{***}$	$0{,}09^{000}$	$1{,}98^{*}$	$1{,}25^{000}$

of the bearded group cannot be ascribed to any assorting mistakes that may have been made, since these plants are very easy to recognize. If we sum up the beardless and the heterozygous plants, we get the segregation 1256 : 368. The agreement with 3 : 1 is not quite satisfactory (expection 1215 : 405; $\chi^2 = 4{,}85^{*}$, $0{,}05 > P > 0{,}02$). Irregularities in the gamete formation may be responsible.

The measurement of the plant height revealed distinct differences between the three groups. The heterozygotes proved highest and they even surpassed both parents. The beardless homozygotes were taller than the bearded ones, but both groups were a little shorter than the corresponding parental types.

As to culm number the heterozygotes also took the first place but were not quite up to the bearded parent. The bearded and the beardless homozygotes were inferior to both parents.

The grain weight and the grain number behaved in a parallel

TABLE 3. *Variation coefficients in the Pansar cross.*

	Height of straw	Culms per plant	Grain weight per plant	Number of grains per plant
Parents:				
Pansar	13,9	62,4	70,9	74,0
Pansar b	10,8	57,7	63,5	64,7
F_2 plants:				
Beardless	13,9	66,7	73,4	81,0
Heterozygotes	9,4	61,4	65,8	64,0
Bearded	14,9	62,2	73,6	76,3

manner, the heterozygotes leading and the beardless homozygotes coming in the last place among the F_2's. The high seed-producing capacity of the bearded Pansar was not quite reached by the heterozygotes.

The heterozygotes consequently showed the highest averages in all the characters investigated. As seen in the lower part of Table 2, the superiority of the heterozygotes was significant in all cases but two, namely *versus* the bearded group in number and weight of grains.

GUSTAFSSON (1946) found in crosses between different chlorophyll lethals in barley that the heterozygotes had a higher variability than the homozygotes. This was not the case in the cross Pansar × bearded Pansar. The variation coefficient was throughout smallest in the heterozygotes. As seen in Table 3, the bearded mutant parent was less variable than the original Pansar.

CONCLUSIONS.

In two different wheat crosses the present writer has found that the heterozygous half-bearded F_2 plants were on an average more vigorous than the corresponding beardless and bearded groups. In the first case two very different spring-wheat varieties, Hindi and Extra-Kolben II, were crossed. In the other one the winter-wheat variety Pansar and its bearded mutant were used as parents. The investigation has provided strong indications of pleiotropic effects of the beardness factor or absolute linkage between this morphological factor and quantitative physiological genes. The last-mentioned cross, where the two parents only differ monofactorially, has also given a very clear demonstration of the existence of a real heterosis stimulation.

When two very different varieties were crossed the average number of culms of the F_2 plants did not reach the mean of the two parents.

In the other cross here reported where the two parents only differ in one single factor (or factor complex) the corresponding differences in vitality were numerically very small and quite insignificant — in accordance with the expectation. These findings are in good agreement with RASMUSSON's (1933) hypothesis on interaction at the manifestation of quantitative characters when a great number of factors are involved. As to plant height the average of F_2 from the first cross is higher than the mean of the two parents. This can be explained by assuming that one of the parents (Extra-Kolben II) includes some strongly dominant length factors, while the other parent (Hindi) has the recessive allels.

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ABSTRACTS — KURZE MITTEILUNGEN

ALBERT LEVAN: The thresholds of colchicine action in barley, rye, diploid oat, and in their artificial tetraploids.

In the autumn of 1944 a few experiments were carried out in order to study the influence of tetraploidy on the activity thresholds of the c-mitosis and the c-tumour reactions. As material for this study two commercial varieties of barley (Opal and Archer), one variety of rye (Steel rye) and one strain of *Avena strigosa* (from Hinneryd, Småland) were selected. Artificial tetraploids of these types were kindly provided by Professor MÜNTZING (barley and rye) and by Dr. FRÖIER (oat). All seeds used in the experiments originated from plants grown the preceding summer under comparable conditions in the Svalöf experimental grounds.

The colchicine treatments were made in the following manner, the diploid of each type and the corresponding tetraploid always being treated simultaneously. Kernels were laid for germination on small canvas frames placed over glass jars containing tap water. When the roots were 1—2 cm in length, the frames were moved over to jars containing colchicine solutions, into which the roots accordingly were submerged. Root-tips were fixed during the first two days for determining the c-mitotic reaction. The remaining roots were left in the solutions until the fifth or tenth day for control of the c-tumour reaction. The following experimental data may be noted.

(1) Opal barley, 2x and 4x. Concentration series: 1, 2,5, 5, 10, 25, 50, 100, 250, 500 $\times 10^{-6}$ mol. Fixing after 15 and 40 hours. Threshold of c-mitosis after 15 hours situated between 100 and 250 $\times 10^{-6}$ mol both in 2x and 4x. After 40 hours 100 $\times 10^{-6}$ mol also showed partial c-mitosis. C-tumours occurred in 2x and 4x from 250 $\times 10^{-6}$ mol upwards after 15 hours, and from 100 $\times 10^{-6}$ mol after 5 days.

(2) Opal barley, 2x and 4x. Concentration series: 60, 80, 100, 120, 140, 160, 180, 200, 220, 240 $\times 10^{-6}$ mol. Fixing after 10 and 36 hours. Threshold of c-mitosis: 60—80 $\times 10^{-6}$ mol after 36 hours. At the earlier fixing (after 10 hours) the 2x showed scattered c-mitoses down to 100 $\times 10^{-6}$ mol and 4x to 120 $\times 10^{-6}$ mol. No c-tumours appeared after 10 hours. After 36 hours incipient c-tumours were found in 120 (2x) and in 140 $\times 10^{-6}$ mol (4x) respectively. After 5 days definite c-tumours were observed both in 2x and 4x as far down as in 80 $\times 10^{-6}$ mol, 2x in addition showed indications of c-tumours even in 60 $\times 10^{-6}$ mol.

(3) Opal barley, 2x and 4x. Experiment designed to study the stimulative region of colchicine. Concentration series: 1, 2,5, 5, 10, 25, 50, 75, 100, 150, 180, 240 $\times 10^{-6}$ mol. The results bearing on the stimulative action on the plant growth will not be dealt with here, but the c-tumour reaction was observed in this series also. After 10 days both 2x and 4x showed c-tumours in 150 but not in 100 $\times 10^{-6}$ mol. The slightly higher value of the threshold may be due to the somewhat different experimental conditions of this series, which was grown in an assimilation box under permanent light. The other series were grown in the laboratory in diffuse light.

(4) Opal barley, 2x. Control series in the experiment with *Avena*

mentioned below under (7). The threshold of c-tumour after 48 hours treatment was between 50 and 75 $\times$ 10^{-6} mol.

(5) Archer barley, 2x and 4x. Concentration series 1, 2,5, 5, 10, 25, 50, 70, 80, 100, 120, 150 $\times$ 10^{-6} mol. Threshold of c-mitosis after 24 hours: 80—100 $\times$ 10^{-6} mol. C-tumours were present in 100 $\times$ 10^{-6} mol after 24 hours and in 70 $\times$ 10^{-6} mol after 3 days. 2x and 4x behaved similarly.

(6) Steel rye, 2x and 4x. Concentration series: 1, 2,5, 5, 10, 25, 50, 75, 100, 150, 200, 250 $\times$ 10^{-6} mol. C-mitotic threshold after 24 hours as well as c-tumour threshold after 24 hours and 4 days: between 75 and 100 $\times$ 10^{-6} mol.

(7) *Avena strigosa*, 2x and 4x. Concentration series: 25, 50, 75, 100, 125 and 150 $\times$ 10^{-6} mol. Both 2x and 4x had the c-mitotic threshold after 24 hours between 25 and 50 $\times$ 10^{-6} mol, and the c-tumour threshold after 2 days between 50 and 75 $\times$ 10^{-6} mol, after 5 days between 25 and 50 $\times$ 10^{-6} mol.

The threshold values of colchicine action met with in the above experiments are summarized in the following table, inserted in which are also the earlier determinations in *Tradescantia* (NEBEL and RUTTLE, 1938), *Allium* and *Pisum* (LEVAN and ÖSTERGREN, 1943), and *Taraxacum* (BENGTSSON and LEVAN, unpublished). All values are expressed in 10^{-6} mol.

Material	C-mitosis	C-tumour
Hordeum	75—100	50—70
Secale	75—100	75—100
Avena	25—50	25—50
Tradescantia	somewhat above 100	—
Allium	100—150	100—150
Pisum (in 0,5 % ethyl-alcohol)	25—75	25—75
Taraxacum	25—50	10—25

The present material shows rather consistently that the diploids and tetraploids of the same plant species have about the same threshold value of the colchicine reactions. In a few cases the colchicine effect appeared one concentration step lower down in the diploids than in the tetraploids, but no significance can possibly be attached to these instances. That the c-tumours in certain concentrations appear earlier and more markedly in the diploids than in the tetraploids, may be connected with the somewhat slower growth of the latter.

In the plants here investigated the tetraploidy has, thus, brought about no appreciable variation in the sensitivity of the plants towards the c-mitosis and the c-tumour reactions.

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ÖIVIND NISSEN: A possible explanation of increased vigour in sib-pollinated later generations after self-fertilisation.

In a paper in this journal GUNNAR NILSSON-LEISSNER (1942) has demonstrated some results from breeding work with *Dactylis glomerata*, showing with significance that sib-pollinated strains of *Dactylis glomerata* are superior to the original I_1 generation. The author explains this phenomenon as a result of natural selection. Without denying the correctness of this theory, I wish to call attention to another possibility that leads to the same improvements. This hypothesis is to the effect that we have a number of incompatability genes linked with vitality genes. If we consider a single pair of incompatability allels, the original plant has the constitution S_1S_2, the I_1 generation consisting of 25 % S_1S_1, 50 % S_1S_2, and 25 % S_2S_2 plants. Even if the incompatability genes are not strong enough to cause self-sterility, we may take it for granted that the progeny of the S_1S_1 plants as well as the progeny of the S_2S_2 plants mostly consists of S_1S_2 plants. Supposing all I_1 plants to give the same amount of seeds, we shall, in the next generation, find more than 50 % S_1S_2 plants. If the S_1S_1 plants and the S_2S_2 plants give only S_1S_2 progeny, the second generation will consist of 12,5 % S_1S_1 plants, 75 % S_1S_2 plants, and 12,5 % S_2S_2 plants. In the third generation we have 62,5 % S_1S_2, and finally we shall reach the equilibrium point at 66,7 % S_1S_2. Supposing that the S_1S_1 plants give more than 50 % S_1S_2 progeny, we shall find the equilibrium point somewhere between 50 and 66,7 % of S_1S_2 plants. At any rate, the generations after sib-pollinating have a higher proportion of plants heterozygous for incompatability genes and for vitality genes linked with the incompatability genes. The more incompatability genes, and the stronger linkage, the greater increase in vigour in the later generations. If we do not get any weakness of the I_1 generation, no increased vigour may be found, and this is in accordance with NILSSON-LEISSNER's results in different other species. If my theory be correct, we shall have the highest degree of heterozygoty and, consequently, the greatest vigour in the first sib-pollinated generation. On the other hand, natural selection will lead to a continuous improvement of the viability. Probably, both of these causes are working, thus, obscuring the effect, and rendering an exact analysis very difficult.

Agricultural College of Norway, Ås, February, 1946.

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